THE EFFECTS OF INVASIVE RATS AND BURROWING SEABIRDS ON SEED AND SEEDLING COMMUNITIES WITH FOCUS ON NEW ZEALAND ISLANDS

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THE EFFECTS OF INVASIVE RATS AND BURROWING SEABIRDS ON SEED AND SEEDLING COMMUNITIES ON NEW ZEALAND ISLANDS

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ABSTRACT

Invasive rats (*Rattus exulans*, *R. rattus*, and *R. norvegicus*) affect vegetation directly through herbivory and indirectly through predation on burrowing seabirds (Procellariiformes: petrels, prions, shearwaters). These seabirds affect vegetation through allochthonous inputs and physical disturbance. I studied the direct impacts of rats on seedling communities on New Zealand islands with three different conditions regarding rats: islands where rats never invaded, islands where rats were present, and islands where rats were eradicated or where populations were low as a result of repeated eradications and reinvasions. I studied a subset of these islands to examine the indirect effects, through predation of burrowing seabirds, of invasive rats on seedlings. I also performed field, laboratory, and greenhouse experiments to determine the mechanisms driving observed patterns in seedling communities. Finally, through a literature review and laboratory trials with *R. norvegicus* I sought to find what plant species and plant parts invasive rats are exploiting and what characteristics may influence herbivorous consumption in rats.

I found that both invasive rats and burrowing seabirds are driving factors for woody seedling communities on New Zealand islands. Woody seedling species richness and density are similar on islands with no history of rats and islands with current rat invasions. However, where rat populations have been historically high but are currently absent or low, seedling species richness is low and seedling densities are high. Low species richness on islands with a history of rats is due to selective consumption of both seeds and seedlings by rats. In addition, the presence of seabirds is associated with high

species richness and density of seeds. However, at very high seabird densities, actual seedling richness and density are low due to extreme physical disturbance. Rats may prefer smaller, fleshy fruits and seeds to seedlings and other vegetative plant parts, but may be deterred from fruit or seed consumption by large size, hard seed coats, or plant chemical defenses. By understanding the separate effects of invasive rats and burrowing seabirds and the mechanisms driving these effects, island restoration efforts can be improved.

TABLE OF CONTENTS

Page

LIST OF FIGURES

Page

LIST OF TABLES

Page

CHAPTER 1: GENERAL INTRODUCTION

Rats (*Rattus exulans, Rattus rattus,* and *Rattus norvegicus*) have been associated with human populations for thousands of years. Through this association rats have spread throughout the world, mainly on ships. Rats are extremely adaptable and have established and maintained populations in almost every terrestrial habitat. However, rat populations on islands can be particularly devastating to native flora and fauna (Atkinson 1985, Courchamp et al. 2003). Island populations of flora and fauna are often unique, in some cases due to isolation from mainland populations. For example, in New Zealand 6% of native vascular plant species are confined to islands (Atkinson 1989).

The isolation of islands makes them good candidates for biological reservoirs. Because of their isolation, invasive eradications, as well as prevention of reintroductions are more feasible on islands than in mainland areas. While there can be inherent problems with sustaining populations on islands, for example population bottlenecks, active management may help mitigate these problems (Atkinson 1989). In New Zealand rats have been eradicated from more than 90 islands (Towns and Broome 2003). While rodent eradication techniques are continually being perfected, our knowledge of restoration techniques after eradications is less complete, especially restoration of plant communities and ecosystem processes. This is due in part to the longer time frame needed for these types of restorations and to a lack of data on pre-invasion states of many islands.

There are three invasive rat species in New Zealand. There is much debate on when *Rattus exulans* arrived on mainland New Zealand islands. However, they were likely present by 1280AD (Wilmhurst et al. 2008) and may have been present earlier

(Holdaway 1999). Some frequently visited offshore islands suffered rat invasions soon afterwards; however, spread to other islands was likely delayed, in some cases until European times (late 1700s; Holdaway 1999). *Rattus norvegicus* was introduced by Europeans in the late 1700s, followed by *Rattus rattus* in the mid to late 1800s (Towns and Daugherty 1994). *R. norvegicus* are excellent swimmers, which enables them to reach more islands than *R. exulans* (Towns and Daugherty 1994, Russel et al. 2005, King 2005). *R. rattus* are excellent climbers, spending most of their time in trees in New Zealand. *R. exulans*, which are also capable climbers, prefer grassland (King 2005). Therefore, the arrival of *R. rattus* devastated native arboreal species in New Zealand (Towns and Daugherty 1994). In total, rodents were introduced to at least 106 New Zealand islands over 5 ha in size (Atkinson 1989). Rats are responsible for approximately 22% of recorded avian extinctions in New Zealand (Atkinson 1985, King 1985). Rats also prey on small mammals, lizards, insects and plants (see review in Atkinson 1985). In addition to decimating many animal populations, rats also affect vegetation in New Zealand (e.g., Campbell and Atkinson 2002, Fukami et al. 2006, Grant-Hoffman et al. 2009). After rat eradications, populations of numerous native plant species show increases in populations (Allen et al. 1994, Campbell 2002).

Rats prey on many different types of animals. However, they are particularly devastating to seabirds, especially small bodied burrowing seabirds (see review Jones et al. 2008). Burrowing seabirds can have dramatic effects on island systems in general and especially vegetation through allochthonous nutrient inputs and physical disturbance (see review Ellis 2005). In general, burrowing seabirds appear to increase density of

vegetation, although this may be suppressed at very high seabird densities (see review in Ellis 2005). In addition, seabirds may increase cosmopolitan or non-native plant species (see review Ellis 2005, Bancroft et al. 2005). Apart from affecting vegetation, seabirds can alter other aspects of island ecosystems, such as soil (e.g. Polis and Hurd 1996, Fukami et al. 2006).

In addition to adding to the body of literature on observed patterns of vegetation differences influenced by burrowing seabirds, this work seeks to add observations of how invasive rats directly influence woody vegetation and to understand the characteristics that determine rat consumptive choices. I sought to understand the mechanisms driving observed associations of change for both burrowing seabirds and invasive rats. Overall, I wanted to address the questions: Are differences in woody seedling communities between islands linked to burrowing seabird density and invasive rat history? If so, which differences can be attributed to burrowing seabirds and which can be attributed to invasive rats? Further, what are the mechanisms driving these linkages? By understanding the mechanisms driving observed vegetation patterns we can better understand underlying ecological processes and better manage islands after rats are eradicated. In addition, while there has been some work on how seabirds affect vegetation (see review in Ellis 2005), less attention has been paid to how invasive rats directly affect vegetation, through consumption of plant parts. With this in mind I wanted to determine what types of vegetation invasive rats are eating and what characteristics these plants have in common that may be driving rat consumptive choices.

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CHAPTER 2: INVASIVE RATS ALTER WOODY SEEDLING COMPOSITION ON SEABIRD-DOMINATED ISLANDS IN NEW ZEALAND[1]

[1]Grant-Hoffman, M.N., C.P.H. Mulder, P. J. Bellingham (2009) Invasive rats alter woody seedling composition on seabird-dominated islands in New Zealand. Prepared for submission in *Oecologia*.

ABSTRACT

Invasive rats (*Rattus rattus, R. norvegicus*) have large impacts on island habitats through both direct and indirect effects on plants. Rats affect vegetation by extirpating burrowing seabirds through consumption of eggs, chicks, and adults. These seabirds serve as ecosystem engineers, affecting plant communities by burying and trampling seeds and seedlings, and by altering microclimate (light, soil properties, and litter). Rats also directly affect plant communities by consuming seeds and seedlings. We studied the direct and indirect impacts of rats on the seedlings of woody plants on 22 islands in northern New Zealand. We compared seedling communities on islands with three different conditions regarding rats: nine islands where rats never invaded, eight islands where rats were currently present, and five islands where rats were either eradicated or where populations were likely to be small as a result of repeated eradications and reinvasions. In addition, we compared plots from a subset of the 22 islands with different burrow densities to examine the effects of burrowing seabirds on plants. We categorized plant communities by species composition and seedling density in a cluster analysis. We found that burrow densities explained more variation in seedling communities than rat status. Seabirds have the greatest effects on seedling survival, and thus density, especially for the smallest seedlings. Species richness and diversity of seedlings, but not seedling density, were most influenced by changes in microclimate induced by seabirds. Seedling density may be driven more by the physical disturbance of seabirds. Islands where rats were eradicated or had low populaitons had the lowest diversity and richness of seedlings, but the highest seedling density. These islands were dominated by

Pseudopanax lessonii and *Coprosma macrocarpa*. Similarly adult plants were less diverse on MANAGED islands. This indicates lasting effects of rats, for at least 20 years, that prevent islands from returning to pre-invasion states.

INTRODUCTION

The ability of predators to shape ecosystems has been recognized for decades (Hairston et al. 1960, Paine 1966, Schmitz et al. 2000, Terborgh et al. 2001). The introduction of a predator can have cascading effects on above and below-ground ecosystem components (Schmitz et al. 2000, Hairston, et al. 1960, Terborgh et al. 2001, Croll et al. 2005, Fukami et al. 2006). Island systems can be particularly vulnerable to invasion and some of the most devastating invasive predators on islands are rats (Rodentia: Muridae; see reviews by Atkinson 1985, Courchamp et al. 2003, Jones et al. 2008). Rats can directly affect systems through consumption of other flora or fauna (Allen et al. 1994, Towns and Daugherty 1994, Campbell 2002). In addition to direct effects, rats affect island ecosystems indirectly by reducing or eliminating seabird populations (Drever and Harestad 1998, Major et al. 2007, Jones et al. 2008). This may have large impacts on other trophic levels, especially when these are burrowing seabirds (order Procellariiformes: prions, petrels, and shearwaters). Burrowing seabirds have been termed 'ecosystem engineers' because of their strong impacts through soil perturbation and nutrient addition (Mulder and Keall 2001, Campbell and Atkinson 2002, Bancroft et al. 2005, Fukami et al. 2006, Wardle et al. 2007).

Rats disrupt seabird driven systems by consuming seabird eggs, chicks, and adults. Seabirds add marine-derived nutrients to soil by feeding at sea and depositing guano at nesting sites on land (e.g. Burger et al. 1978, Mizutani and Wada 1988, Wainwright et al. 1998, Anderson and Polis 1999, Hawke and Newman 2004). In

addition, burrowing seabirds contribute dead chicks, egg shells, and occasionally dead adults, which increase N and P available to plants by increasing rates of deposition in the soil (Furness 1991). However, guano deposition also lowers soil pH (Ward 1961, Okazaki et al. 1993, Mulder and Keall 2001), potentially reducing nutrient availability to plants (Blakemore and Gibbs 1968, McLaren and Cameron 1990). In addition, trampling and burrowing activity can change litter levels and soil structure, decreasing seed germination and seedling survival (Gillham 1961, Campbell 1978, Maesako 1999, Mulder and Keall 2001, Ellis 2005). Seabirds influence plant composition and abundance in many areas where they are found (see review Ellis 2005).

Three *Rattus* species readily invade novel ecosystems: *R. exulans* (Pacific rat or Kiore), *R. rattus* (Ship rat), and *R. norvegicus* (Norway rat) (Atkinson 1985). Since the mid-1800's approximately 45 island groups have been invaded by rats (*Rattus rattus, R. norvegicus*) worldwide (Atkinson 1985, Thorsen et al. 2000). Rats consume seeds, seedlings, and adult plant parts in addition to fauna (Campbell 1978, Campbell et al. 1984, Wilson et al. 2003). Woody vegetation may be particularly vulnerable to invasive rats (Gillham 1961, Maesako 1999, Mulder and Keall 2001). During the past decade numerous projects have focused on eradicating rats (Towns and Broome 2003). A recent review reported 332 successful rodent eradications from 284 islands covering a total of 47,628 ha (Howald et al. 2007). Such eradications are often followed by the reintroduction of native species. However, the removal of rats does not necessarily result

in the rapid return of seabird colonies (Gaze 2000, Miskelly and Taylor 2004), resulting in islands that lack both rats and seabirds.

The flora and fauna of New Zealand are especially vulnerable to rats because they have evolved for the last 16 million years in the absence of terrestrial mammals except bats (King 2005, Worthy et al. 2006). We studied 22 islands off the coast of the North Island of New Zealand with different histories of invasions by either ship rats or Norway rats. Some of these islands have never been invaded by rats (UNINVADED islands), some had current rat infestations at the time of our study (INVADED islands), and on some islands rats had been eradicated entirely or repeatedly eradicated after subsequent reinvasions, keeping populations low (MANAGED islands). We examined both direct and indirect effects of invasive rats on the woody seedling community on islands. We evaluated the following hypotheses:

1. Seabird density and rat history will affect the woody seedling community (especially small seedlings): seedling density, species richness, and diversity. Small seedlings will be most vulnerable to both invasive rats and burrowing seabirds.

We predicted that seedling communities would be similar on islands with similar rat history and burrow densities due to similar pressures of consumption, nutrient addition, and disturbance.

We expected high plant species richness and diversity on islands with intermediate seabird densities (intermediate disturbance hypothesis, Connell 1978). At intermediate burrow densities abundant nutrients along with some

trampling and disturbance may increase species richness and diversity of plant communities. We also expected fewer plants and fewer plant species at very high seabird burrow densities. High levels of burrowing and trampling increase disturbance and damage to plants, limiting plant growth (Maesako 1999). Further, high nutrient levels in the presence of high densities of seabirds may contribute to low plant species richness and diversity (Tilman 1982).

We expected community differences to be greatest for the smallest size class of seedlings, since these would be most vulnerable to partial consumption by rats and physical disturbance by seabirds.

2. Seedling composition and abundance on islands where rat populations are low or have been eradicated, but on which seabirds have not yet returned, will continue differ from uninvaded islands.

We did not expect seedling communities on MANAGED islands, where eradications or eradication attempts have taken place within the last 25 years, to revert to pre-invasion states, partly because some impacts of rats may take decades to reverse: for example, shifts in the relative abundance or even the complete absence of seeds in the seed bank following selective herbivory. In addition, many of the impacts of rats are mediated by seabirds. Seabirds are philopatric and once removed from islands may take many years to return, or need careful translocations to re-establish populations (Warham 1990, Miskelly and Taylor 2004, Priddel et al. 2006).

3. Certain plant species will be most impacted by the effects of both invasive rats and burrowing seabirds.

Previous studies in New Zealand have noted sensitivity of certain tree species (*Coprosma macrocarpa,* Rubiaceae; *Dysoxylum spectabile*, Meliaceae; *Melicytus novae-zealandiae,* Violaceae; *Pittosporum crassifolium,* Pittosporaceae; *Pseudopanax lessonii,* Araliaceae; *Streblus banksii*, Moraceae) to invasive rats (Atkinson 1985, Campbell and Atkinson 1999, 2002). The sensitivity of these species is attributed to consumption of plant material by invasive rats. There are no reports of benefits of invasive rats to plant species. Therefore, in addition to expected negative effects to plant species, we also considered possible positive effects to plant species of rat invasion or eradication.

4. Microsite variables driven by seabirds, and biogeographical variables not driven by seabirds, will be associated with differences in seedling communities: species richness, diversity, and seedling density.

Burrowing seabirds affect small-scale physical variables in this system such as soil pH, total N and Olsen's P concentrations, and canopy density (Fukami et al. 2006, Mulder et al. 2008), and we expected these variables to affect seedling density, species richness, and diversity. In addition, biogeographical variables (island area, distance from mainland, and climate) will influence seedling communities (MacArthur and Wilson 1967).

In order for island restoration programs to be effective we need to understand both the impacts of seabirds and their predators on vegetation, and the mechanisms through which these impacts occur. This study contributes toward this goal by elucidating the relative importance of direct impacts of rats and understanding which of these can be reversed by rat removal. In addition we seek to understand the indirect effects of rats (through extirpation of burrowing seabird colonies). This type of information should allow us to move beyond the eradication of rats toward active restoration programs.

METHODS

Study area

We established study plots on 22 islands (3 to 350 ha) in warm temperate northern New Zealand (Table 2.1). All islands are within 48 km of the North Island and most are of volcanic origin (Table 2.1). Islands fell into one of three groups based on rat status: those with rats present (INVADED), those where rats were never present (UNINVADED), and those where rats have been successfully eradicated or repeatedly eradicated after subsequent reinvasions (MANAGED). It is likely that all islands had colonies of burrowing seabirds (petrels, shearwaters, prions) before the introduction of ship and Norway rats (Holdaway 1999, Worthy and Holdaway 2002). However, definitive evidence is often lacking. Furthermore, the time since extirpation on island where seabirds are no longer present is often unknown, but is <170 years ago (the time since European colonization). Due to the similarities in behavior of the seabird species, the difficulty in determining with certainty the species of historical seabird populations, and overlap in forest use by some seabird species, we did not distinguish between seabird species.

Seedling counts and physical measurements

We sampled plots (10 m × 10 m) in mature stands of secondary coastal forest (Court et al. 1973, Atkinson 2004) on each island between late January and mid April in 2004 and 2005. On islands with seabirds, two plots were placed within seabird colonies (areas with relatively high densities of seabird burrows) and two were placed in areas with few or no seabird burrows. We established four plots on island without seabirds.

Within all plots we positioned 21 regularly-spaced 1 m^2 subplots (9 subplots in 2004 using a stratified random sampling design: data used for cluster analysis only). Within each subplot, we identified all seedlings of woody trees to species and counted seedlings in five height classes (0-15 cm, 16-45 cm, 46-75 cm, 76-105 cm, 106-135 cm). We measured and identified all adult trees and stems $\geq$ 2.5 cm dbh (diameter at breast height, 1.5 m) in all plots. Other vascular plants in plots included ferns, grasses, sedges, and mostly non-native herbaceous species. For analyses we used the more extensive dataset from 2005, but to maximize the number of species we combined data from 2004 and 2005 for the cluster analysis.

Measurements of soil temperature (using a HANNA Instruments HI 145 digital thermometer inserted to approximately 10 cm depth), soil moisture (using a Delta-T thetaprobe inserted approximately 6 cm depth), canopy cover (using a spherical densiometer; Forest Densiometers, Bartlesville, OK), and a litter sample from a 0.1m^2 area were taken in every third subplot (7 samples per plot). Five hemispherical photographs were taken at the four corners and at the center of each plot from which earth cover (vertically projected canopy area per unit ground area, Hemiview canopy analysis software, Delta-T Devices Inc., Houston, TX) was estimated. We also measured mean air temperature and relative and absolute humidity using dataloggers (Hobo H8 ProTemp / RH dataloggers, Onset Computer Corporation) on two plots per island (2004–05). Soil compaction was measured from the surface of the ground at 10 random points in most plots using soil compaction tester (Dickey-John Corp. Auburn, IL). We counted all burrow entrances within the 100 m^2 plot as an index of seabird density, but the ratio of

entrances to actual burrows is probably not one to one (as there may be multiple burrow entrances or unused burrows) and may differ slightly for different bird species (Warham 1990). Island area and distance to mainland were obtained from the Rodent Invasion Project sponsored by the Auckland University Department of Statistics (http://www.stat.auckland.ac.nz/research/rodent-invasion/map/, downloaded January 2008). Rat status (INVADED, UNIVADED, MANAGED) was based on the knowledge of New Zealand Department of Conservation staff who monitor and maintain bait stations placed on the islands.

Statistical Analyses

Similarity and recovery of woody seedling communities

Hierarchical cluster analyses were performed to determine whether the composition and density of seedling and adult vegetation communities would lead to island groupings consistent with rat history or seabird density. We used McQuitty's similarity analysis, a weighted average linkage method (Anderberg 1973, SAS Institute 2002). Islands were grouped using counts of woody seedlings by species from both years. This produced a tree diagram, which was overlaid with both seabird burrow density and rat status (Fig. 2.1). R^2 values were used to indicate how much of the variation is explained by the groupings.

The highest densities of seabirds occur on UNINVADED islands; thus, seabird density and rat status are confounded. We performed analyses at two scales: within islands and among islands. Within islands there is variation in burrow density as these

birds are colonial nesters and burrows are aggregated in space, but rat status and other island level characteristics (such as island size and distance to mainland) are constant. At this scale we looked at a subset of 12 islands that had variation (at least 5 burrows between the highest and lowest density plots) in burrow density. Plots were the experimental unit (n=42), and we used means per plot for response variables. We used regression (PROC GLM in SAS; SAS Institute 2002) to examine the relationships between explanatory variables (burrow density and burrow density squared, to test for non-linearity) and the response variables (woody seedling density per m^2, species richness per plot, and species diversity Shannon-Weiner diversity index, H′). The model for the within-island scale also included islands as blocks. At the among-island scale, islands are the unit of analysis and independent replicates. At this scale we separated the effects of rats into indirect effects (via changes in seabird burrow density) and direct effects (impacts not explained by seabird density) by running ANOVAs (sequential SS) including burrow density, burrow density squared (to test for non-linearity), and rat status (a fixed variables with three levels: UNINVADED, MANAGED and INVADED). Island size was included as a covariate. For these analyses the experimental unit was the island, and the mean per island across all subplots was used (n=22). To account for differences in seedling densities we performed rarefaction analysis for species richness and diversity at both sampling scales (Gotelli and Entsminger 2006). Since cluster analyses indicated strong differences in composition between plots with fewer than 0.05 burrows m^2 and those with more than 0.05 burrows m^2 we used this categorization. The cluster analysis also showed a split between islands with 0.5 burrows m^2; but since all plots with 0.5

burrows m^2 were located on two islands, these plots were not classified separately. At the among-island scale we also examined adult woody species richness and diversity as response variables to determine the extent to which patterns found at the seedling stage were likely to be maintained as plants aged.

In each of five height classes we examined the relationship between seedling density per m^2 and burrow density and rat status via protected ANOVAs (Scheiner 2001). We performed a MANOVA including all height classes followed by ANOVAs for each class if the MANOVA was significant.

Woody plant species

We examined differences in seedling densities for those plant species that were present in at least four plots (within-island scale) or four islands (among-island scale). We tested for significant differences in seedling densities explained by differences in burrow densities (within-islands) or rat status (among-islands) using the same models as for the community-level data. A few species (*Coprosma repens, Melicytus ramiflorus, Pittosporum crassifolium, Streblus banksii;* scientific names follow http://nzflora.landcareresearch.co.nz, downloaded January 2008) showed strongly binomial responses. For these species we performed G-tests at the among-island scale (to determine if the presence of seedlings was independent of rat status) and logistic regressions at the within-island scale (to determine whether burrow density explained species presence).

To identify species for which seedling densities were much greater or smaller than expected based on seed source (abundance of mature trees), we graphically compared the ratio of adults to seedlings for species that were significantly affected by rat status or burrow density (graphs not shown). Counts of seedlings and adults were standardized by dividing by the mean counts from all islands, and plotted on a log scale. This allowed us to identify islands with particularly high or low numbers of individuals (both adults and seedlings) of a species relative to other islands, as well as to identify islands where seedling numbers were high or low relative to adult densities. However, these are indications only and not definitive due to the limited sampling of the adult communities.

Microsite and biogeographical variables

To determine whether environmental variables could explain variation in seedling density, species richness, and species diversity we used an information-theoretic approach (Akaike 1973, Burnham and Anderson 2002, Stephens et al. 2005). Candidate variables included four microsite variables known to be affected by seabird density that have the potential to affect seedling growth and survival (canopy density, soil pH, total soil N concentration, and soil Olsen's P concentration; Fukami et al. 2006, Mulder et al. 2008); and five microsite variables potentially affected by seabirds (soil compaction, soil moisture, soil temperature, canopy density at ground level, and litter weight). In addition, since some variation may be driven by biogeographical variables such as climate or island location and are unlikely to be driven by seabird densities or rat status, we included six additional variables (June and July mean temperature, June and July relative

humidity, island area, and distance to the mainland). We selected among competing models using Akaike's Information Criteria (Akaike 1973) adjusted for small sample size (AIC_c, Burnham and Anderson 2002). We report results and parameter estimates for all models not distinguishable from the best model (AIC_c <2). Data sets for soil compactions and ground-level canopy cover were incomplete. However, since running the subset of plots for which they were available resulted in their exclusion from the top models, we re-ran the analyses excluding these two variables and including all plots.

RESULTS

Similarity and recovery of woody seedling communities

When burrow density was overlaid on the islands clustered by seedling communities, islands generally grouped by burrow density (Fig. 2.1). The first delineation, explaining most of the variation (R^2=0.65), was between two highly burrowed UNINVADED islands (Middle Island, 0.52 burrows m^{-2}; Green Island 1.01 burrows m^{-2}) and all other islands. The next clear delineation was between the remaining islands with a burrow density > 0.05 burrows m^{-2}, and those islands with a burrow density < 0.05 burrows m^{-2} (an additional 10% of variation explained). When rat status was overlaid on the cluster diagram, INVADED islands and most UNINVADED islands were clustered together, whereas MANAGED islands were interspersed throughout these two categories (Fig. 2.1). Overall, the location of the MANAGED islands in the diagram was better explained by their seabird densities than by their rat status: the two MANAGED islands that clearly fell within the UNINVADED group, Otata (0.07 burrows m^{-2}) and Whenuakura (0.15 burrows m^{-2}), also had the highest burrow densities of the MANAGED islands. The three islands with very low burrow densities (mean <0.04 burrows m^{-2}, despite a long history of eradication or control) were adjacent to INVADED islands in the diagram. Adult communities showed no consistent patterns relative to rat status or burrow density (data not shown).

At the within-island scale seedling density showed a marginal linear decrease with increasing burrow density ($F_{1,11}$=2.97, P=0.09). This increase in seedling density with increasing burrow density also held for height classes (MANOVA; Roy's greatest

root, $F_{5, 24}$=2.08, P=0.10), and seedlings in two of the five height categories significantly decreased with increasing burrow density (height class 0.16 m-0.45 m, $F_{1,28}$=3.65, P=0.07; 0.46-0.75 m, $F_{1,28}$=9.00, P=0.006, Fig. 2.2). However, the data in these analyses exhibited an envelope effect (Goldberg and Scheiner 2001) with seedling density either high or low at low burrow density, but consistently low at higher burrow density (above 0.2 burrow m^{-2} seedling density dropped to 2 seedlings m^{-2} or lower). Therefore, we examined maximum seedling density values for burrow intervals (5 burrows per interval) and found a strong negative relationship between burrow density and seedling density ($F_{1,11}$=20.9, p=0.001; Fig. 2.3). Seedling species richness and H′ were not explained by burrow density at the within-island scale (P>0.6 for both), nor did rarefaction results show a difference between low (0-0.05 burrows m^{-2}) and high (over 0.05 burrows m^{-2}) burrow densities (95% confidence intervals overlapping).

At the among-island scale, rat status marginally explained seedling density once burrow density was included in the model ($F_{2,16}$=2.72, P=0.10). Seedlings were more abundant on MANAGED islands than on either INVADED or UNINVADED islands, and this was driven by small seedlings (MANOVA for height classes; Roy's greatest root, $F_{5,13}$= P=0.03; ANOVA <15cm; Fig. 2.3: $F_{2,16}$=4.67; P=0.02). At the among-island scale, there was no significant effect of seabird burrow density on seedling density in height classes (P>0.4). Despite the greater number of seedlings, both H′ ($F_{2,16}$=4.20, P=0.03) and species richness ($F_{2,16}$=10.3, P=0.001) were significantly lower on MANAGED islands (Fig. 2.4a). Rarefaction results also showed lower species richness and H' on MANAGED islands, which became more pronounced as sample size increased (Fig. 2.4b, only species

richness shown). In general, there were few differences between INVADED and UNINVADED islands in seedling compositional variables, while MANAGED islands were different from the other two groups in most respects.

The opposite trends for seedling density and diversity suggests that one or a few plant species perform exceptionally well when rats are eradicated and seabird burrow densities are low (indicating that seabird colonies have not fully recovered). This was supported by a closer examination of relative abundance of individual species. On MANAGED islands one or two species accounted for between 78% and 94% of the seedlings found. *Pseudopanax lessonii* was the dominant species (38-94% of seedlings) on four of the five MANAGED islands, while the fifth island, Te Haupa, was dominated by *Coprosma macrocarpa* (78%).Other dominant species on MANAGED islands included *Pittosporum crassifolium*, *Dysoxylum spectabile*, and *Macropiper excelsum* s.l.

Burrow density did not explain species richness, or H′ for mature trees ($P>0.1$ for both). However, adult vegetation showed the same trends as the seedling community with respect to species diversity and density and rat status: INVADED and UNINVADED islands were generally similar ($H'=1.30$ and 1.43; SD = 0.33, 0.44: species richness = 8.33, 8.12; SD=2.45, 3.27 respectively) while MANAGED islands had lower values ($H'=0.92$, SD=0.46; species richness=1.52, SD=3.27), although these differences were not significant ($P=0.07$ for both).

Woody plant species

Sixteen of 31 woody species were present as seedlings in at least four plots at the within-island scale, and fifteen of 31 species were present on at least four islands at the among-island scale. At the within-island scale a MANOVA of all species simultaneously was not significant (P>0.2), so no further analyses were performed. However, results for logistic regression showed that *Coprosma repens* increased with increasing burrow density ($\chi 2_{(1)} = 6.29$, P=0.01)

At the among-island scale, densities of individual species were not explained by burrow density. This may be due to low sample numbers per individual plant species. However, rat status was significant (Roy's greatest root, $F_{15,3}=14.88$, P=0.02) and was analyzed further. As we expected, different trends were seen for different species. *Pseudopanax lessonii* seedlings were significantly more abundant on MANAGED islands than on INVADED or UNINVADED islands ($F_{2,16}=5.92$, P=0.01), and adults showed a similar trend. We found an average of 21 *Pseudopanax lessonii* adults per MANAGED island versus five and four adults for UNINVADED and INVADED islands respectively. Results from G-tests showed that seedlings of *Melicytus novae-zealandiae* ($\chi 2_{(2)}=13.28$, P=0.001) and *Streblus banksii* ($\chi 2_{(2)} = 10.03$, P=0.007) were most abundant on UNINVADED islands and were absent from plots on MANAGED and INVADED islands. Mature trees of *Streblus banksii* were also more abundant on UNINVADED islands than on other islands. We found an average of eight adult *Streblus banksii* per 10 m^2 plot on UNINVADED islands compared to no adults on MANAGED islands and only one adult on all eight INVADED islands. Three other species showed marginal relationships with rat status: *Pittosporum crassifolium*

($\chi 2_{(1)} = 4.97$, P=0.08) was more abundant on UNINVADED and MANAGED islands and less abundant on INVADED islands; *Geniostoma ligustrifolium* ($F_{2,16}$=3.31, P=0.06) was most abundant on INVADED islands and scarce elsewhere; *Macropiper excelsum* s.l. ($F_{2,16}$=2.76, P=0.09) was also most abundant on INVADED islands.

Microsite and biogeographical variables

Generally, the best models explaining seedling community characteristics included more microsite factors than large scale or biogeographical factors (Table 2.2). However, there was a significant positive relationship between June air temperature and burrow density ($F_{1,15}$=8.49, P=0.011). Islands with many seabirds tended to be warmer in winter. All but one microsite variable (canopy density) were included in a best model for at least one of the response variables.

The best four models for seedling density included two out of six large scale and biogeographical variables (June air temperature, island area) and four microsite variables, although for only one of these (soil temperature) was there strong support (95% confidence intervals did not overlap with zero). The variables selected explained more of the variation in seedling species richness and H′ than they explained seedling density. The best models for species richness included strong support for a negative relationship with summer absolute humidity and distance to the mainland as well as for negative relationships with soil pH and total soil N concentration, while diversity was driven by summer temperature (positively), humidity (negatively), and island area (positively), but also by litter weight, soil pH, soil total N and Olsen's P concentrations (all negatively).

Results from biogeographical variables, such as distance to mainland, agreed with predictions from island biogeography theory (MacArthur and Wilson 1967). Some microsite variables, including soil N and P concentrations, agreed with expected results based on known seabird effects while others like soil pH and moisture did not.

DISCUSSION

Similarity and recovery of woody seedling communities

Our study showed that similarity in seedling community composition on islands in New Zealand was determined primarily by the burrow density of seabirds. Conversely, rat status of islands was not consistently a predictor of seedling communities. Our results suggest that burrowing activity is determines seedling density. At very high seabird burrow densities (>50 burrows per 100 m^2) woody seedling density is low, and woody seedling survival may be more a function of chance and less dependent on competition based on seed or seedling characteristics. Under this disturbance regime species that can maintain their populations primarily through vegetative reproduction may have an advantage. We found that smaller seedlings (those < 75 cm in height) were more dramatically affected than larger seedlings; and smaller seedlings may be particularly susceptible to death by trampling or burrowing. These data also support the notion that seabirds are acting as the limiting factor for plant regeneration at the early stages, most likely through trampling and uprooting of seedlings and burial of seeds during burrow formation (Furness 1991, Campbell and Atkinson 2002). However, by the time seedlings reach 75 cm in height, the negative impacts of high burrow density are no longer discernible, and larger seedlings may not be as vulnerable to seabird disturbance.

Rat status of islands was also linked to seedling density, with higher seedling density on MANAGED islands than on INVADED or UNINVADED islands. This result likely reflects the recovery of *Coprosma macrocarpa*, *Pseudopanax lessonii*, and other plant species after rat eradication. Other studies have also found that seedling numbers on New

Zealand islands increase after eradication of *R. norvegicus* (Allen et al. 1994). In addition, *R. exulans,* a related species, reduces recruitment and establishment of many New Zealand tree and shrub species through consumption of seeds and plant parts (Campbell and Atkinson 1999, Campbell and Atkinson 2002, Campbell 2002).

Contrary to what we expected, we found no significant effects of burrow density on species richness or diversity at the within-island or among-island scales. However, for both analyses this may be due to a lack of power to detect differences between low and intermediate burrow densities. At the within-island scale we restricted our analyses to the subset of islands for which there was considerable variation in burrow density. This resulted in the exclusion of islands with few seabirds. At the among-island scale we looked at the effects of burrows after considering the effects of rats. Since these variables are partially confounded this analysis compared plots on islands with an overall low seabird burrow density (INVADED and MANAGED islands) or an overall high seabird burrow density (UNINVADED islands), but not between these two groups. The cluster analysis suggested large changes around a threshold of 0.05 burrows m^{-2}, and additional analyses support this trend for diversity (Mulder et al. 2008).

We did find effects of rat status on species richness and diversity after accounting for burrow density. Seedling species diversity and richness were higher on INVADED and UNINVADED islands than on MANAGED islands, while seedling densities were lower than on MANAGED islands. INVADED and UNINVADED islands were similar in species richness and diversity. On MANAGED islands the removal of burrowing seabirds allows seedling density to increase. Further, a release from the herbivorous pressures of rats may allow

competitive dominants to flourish (see review in Olff and Ritchie 1998). Finally, selective consumption by rats may lead to missing species from the seed bank contributing to low species richness and diversity on MANAGED islands. Combined these things lead to islands with high seedling density, but low seedling richness and diversity. Consequently, mature forests on MANAGED islands may have low species richness and diversity compared with INVADED or UNINVADED islands (as suggested by the consistent patterns up to sapling sizes and the low species richness and diversity on MANAGED islands in adult vegetation). The effects of rats are lasting and will persist through adult woody plant communities. Thus, plant communities on MANAGED islands are not reverting to communities similar to those on UNINVADED islands.

Woody plant species

Six of 16 woody plant species tested showed at least marginal associations with rat status. Four of the species tested (*M. novae-zealandiae, P. crassifolium, P. lessonii,* and *S. banksii*) have been previously identified as species that are sensitive to predation by another rat species (*Rattus exulans*, Atkinson 1985, Campbell and Atkinson 1999, 2002). In our study we found strong support for direct rat predation on two species: *S. banksii* and *M. novae-zealandiae*, which were entirely restricted to UNINVADED islands, except for trees found on Motueka, an island with an active burrowing seabird population. Neither *S. banksii* nor *M. novae-zealandiae* were found on MANAGED islands as adults or seedlings, and both of these plants have fleshy seeds which may be vulnerable to rat consumption. *P. crassifolium* was present as both adults and seedlings

on MANAGED islands and had comparatively high numbers of seedlings (relative to adults) on these islands. *P. crassifolium* is consumed by both *R. exulans* and *R. norvegicus* (Campbell and Atkinson 1999, Moors 1985) and in the case of *R. exulans* low recruitment of this species has been attributed to seed consumption (Atkinson 1978). Although this seed is clearly eaten by rats (personal observation), this species, compared to *S. banksii* and *M. novae-zealandiae*, seems to do well once rats are removed and does not appear to suffer from lasting effects of rat consumption.

While we did not find clear evidence for positive effects of rats on plant species, we did find several species that recovered well once rats were removed from an island. *C. macrocarpa, D. spectabile, Macropiper excelsum, Pseudopanax lessonii,* and *Pittosporum crassifolium* had numerous seedlings on MANAGED islands. Unlike *S. banksii* and *M. novae-zelandia* these species are recovering well after rat eradications. These species may be consumed by rats, but this consumption may not be as devastating as for other species. For example, *R. exulans* (a smaller rat species than those on our study islands) consume leaves and bark of *P. lessonii*, but they do not appear to eat the fruit or seeds (Campbell and Atkinson 1999); and suppression of this species may take place at the seedling rather than the seed stage. *R. exulans* also suppresses the recruitment of *C. macrocarpa* and *D. spectabile* (Campbell and Atkinson 2002) and in the case of *C. macrocarpa* consumes the fruit, bark, twigs, and seedlings (Campbell 1978, Campbell et al. 1984). Maintenance of viable seeds in the seedbank and rapid regeneration of these species following the removal of rats may play a role in their recovery. This may be accomplished through copious seed production or quick germination. *P. lessonii*

regenerates frequently after disturbance (burning, herbivory) (Campbell and Atkinson 1999). It has also been postulated that *C. macrocarpa* and *D. spectabile* seeds are merely quiescent (not dormant) and can germinate readily after seed fall (Fountain and Outred 1991), potentially out-competing slower germinating species if the pressure of rat consumption is removed. Evidence from the seedling community suggests that rat removal will result in a community with a very different composition than on islands with current rat invasions or on islands where no rats have invaded.

Overall, there was more evidence for direct impacts of rats on seedlings of individual species than for indirect impacts mediated through seabird densities, and only one of 16 species showed a relationship with seabird density. *Coprosma repens* increased with increasing burrow density. It is an early successional species that is often prostrate (Poole and Adams 1964). In heavily burrowed areas trees will often topple over, and those that can re-grow from this position have an advantage (Cameron 1990, Bellingham and Sparrow 2000). The reported sensitivity of *C. repens* to rat effects (Campbell and Atkinson 2002) may be the result of positive impacts of high seabird densities (as described above), which occur only where rats are absent.

Microsite and biogeographical variables

In general we found that microclimate and biogeography effects explained more variation in species richness and diversity than in seedling density. Soil N and P concentrations were included in the best models for species richness and diversity, but not seedling density (as expected if this variable is driven by seabird disturbance). In both

cases the relationship was negative. This indicates that species richness and diversity decreased with increasing soil N and P concentrations, consistent with previous studies (Tillman 1982). This may be due to competitive dominants using these resources and reducing species richness (Tillman 1982). In addition, very high nutrient inputs and low soil pH can inhibit seed germination and seedling growth (Hilhorst and Karssen 2000). At out study sites there appear to be few plants that can withstand these very high nutrient loads coupled with the physical disturbance of burrowing activities.

Both the predatory effects of rats through reductions in seabird densities and the herbivorous effects of rats through seed and seedling consumption shape the seedling communities of New Zealand islands. Seabird burrow density generally impacted seedling communities in a non-species specific way, and there seems to be a threshold of burrow density below which the seedling community changes. Restoration of seabirds to islands where they have been extirpated by rats may be necessary to restore island vegetation. Rats, on the other hand, are important for specific species and have large negative impacts on some species, while other species benefit from rat eradication. By incorporating a better understanding of how invasive rats are affecting island vegetation, restoration programs can better reach goals to manage diversity and richness of the flora and fauna of islands.

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Table 2.1. Islands studied during 2004 and 2005, '*' indicates islands used for within-island analyses. All islands are located off the North Island of New Zealand. Seabird densities are based on means of two to four 100 m^2 plots.

Island	Island abbreviation	Latitude (°S)	Longitude (°E)	Area (ha)	Distance from mainland (km)	Rat History	Rat Status	Seabird density (burrows/100m²)
*Ohinauiti	OHI	36.71	175.88	5.9	5.3	Uninvaded	Uninvaded	3.5
*Aorangia	AOA	35.48	174.71	5.6	21.4	Uninvaded	Uninvaded	11.0
*Ruamāhauiti	RTI	36.97	176.06	25.5	18.1	Uninvaded	Uninvaded	13.0
*Aorangi	AOI	35.48	174.72	107.1	20.6	Uninvaded	Uninvaded	17.0
*Ruamāhaunui	RNI	36.95	176.09	32.4	19.9	Uninvaded	Uninvaded	18.5
*Tawhiti Rahi	TR	35.45	174.71	158.2	21.7	Uninvaded	Uninvaded	24.5
*Archway	ARY	35.49	174.74	6.3	20.7	Uninvaded	Uninvaded	38.0
*Middle (Atiu)	MID	36.6	175.84	13.5	8.3	Uninvaded	Uninvaded	68.5
Green	GRN	36.64	175.85	2.5	7.2	Uninvaded	Uninvaded	101.5
Motukaramarama (Bush)	MOA	36.68	175.37	10.1	3.3	*Rattus norvegicus*	Invaded	0
Motuoruhi	MOI	36.73	175.4	58.0	2.6	*Rattus rattus* or *R. norvegicus*	Invaded	0
Motutapere	MOE	36.78	175.4	45.6	2.5	*Rattus rattus* eradicated 1996, reinvaded	Invaded	0
Pakihi (McCallum)	PAK	36.54	175.1	110.0	1.4	*Rattus rattus* or *R. norvegicus*	Invaded	0
Rakitu (Arid)	RAK	36.07	175.3	350.0	37.6	*Rattus rattus*	Invaded	0
Aiguilles	AIG	36.03	175.39	72.7	47.7	*Rattus rattus*	Invaded	0.5
Goat	GOT	36.26	174.8	13.4	0.015	*Rattus rattus*	Invaded	0.5
*Motueka	MOK	36.82	175.8	6.2	1.2	*Rattus rattus* or *R. norvegicus*	Invaded	4.0
Te Haupa	TH	36.51	174.74	6	10.5	*Rattus norvegicus eradicated 1989, Mus musculus*	Managed	0.25

Table 2.1 Continued

Hauturu	HAU	37.21	175.89	10.3	0.5
*Motuhoropapa	MOP	36.41	174.57	8.6	17.9
*Otata	OTA	36.41	174.58	15	17.5
*Whenuakura	WHE	37.22	175.89	3	0.9

Rattus norvegicus eradicated 1985, Mus musculus	Managed	1
Rattus norvegicus erradicated 1987, 1991	Managed	2
Rattus norvegicus erradicated 1987, 1991	Managed	7
Rattus norvegicus eradicated 1985	Managed	15.25

Table 2.2. Variables included in the best models based on AICc scores for three response variables (seedling density per m^2, plant species richness, and plant species diversity, H′). Positive and negative signs indicate the direction of parameter estimates for a variable included in models within 2 of the lowest AICc value; 'NE' indicates a variable that did not enter the model. Cells shaded in grey indicate a parameter estimate with a 95% confidence interval that does not overlap with zero.

	Seedling Density (4 models)	**Species richness (6 models)**	**Diversity, H′ (7 models)**
Range of R^2 values for top models	**0.41 – 0.44**	**0.58 – 0.65**	**0.59 – 0.70**
Jan absolute humidity	NE	-	-
Jan average air temperature	NE	NE	+
June absolute humidity	NE	NE	NE
June average air temperature	-	NE	NE
distance to mainland	NE	-	-
island area	-	+	+
soil moisture	+	+	NE
soil temperature	+	NE	-
canopy density	NE	NE	NE
litter weight	+	-	-
soil pH	+	-	-
soil total N	NE	-	-
soil Olsen P	NE	-	-

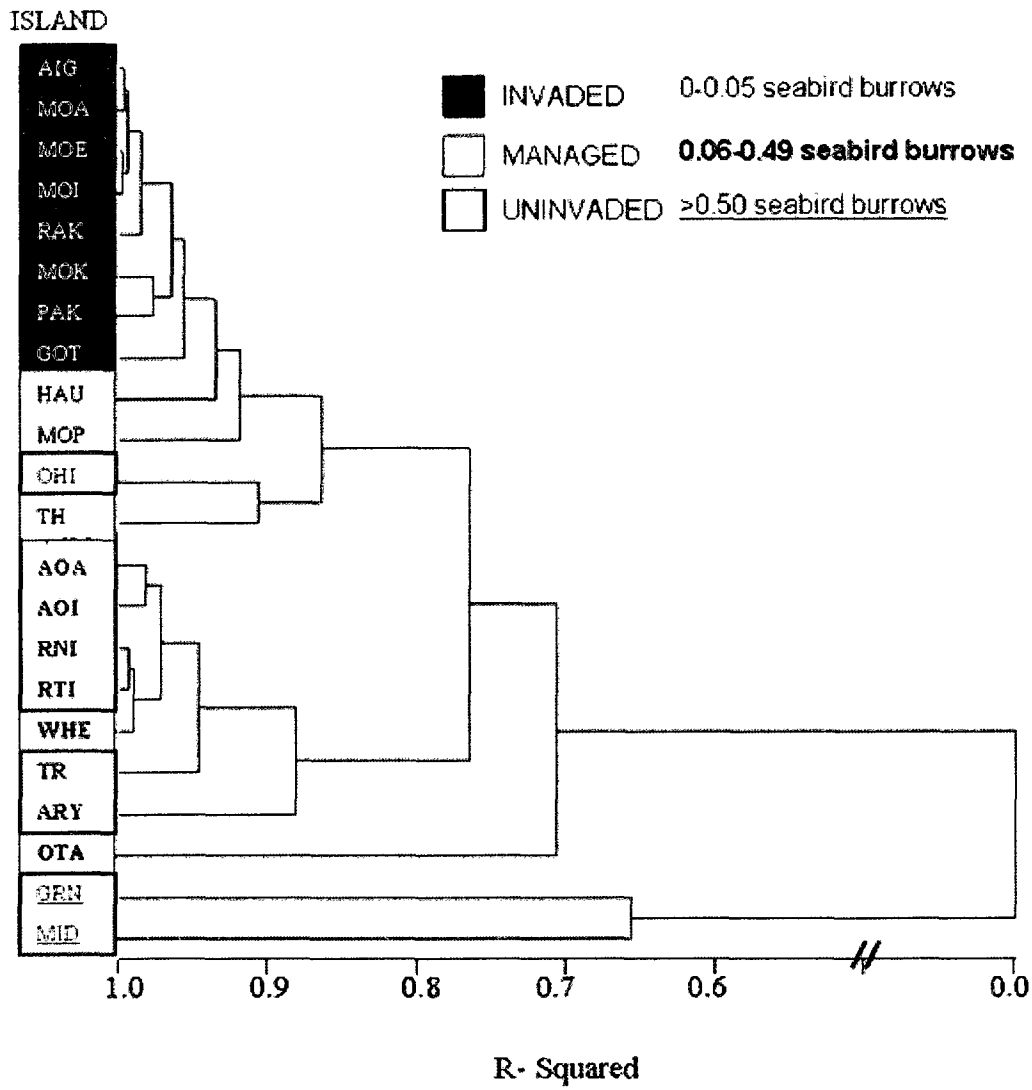
FIGURE LEGENDS

Fig. 2.1. Hierarchical cluster analysis using McQuitty's similarity analysis (SAS Institute 2002) on means of woody seedling counts by plant species. R^2 represents the proportion of the variance accounted for by the clusters. Island names are abbreviated; see Table 1 for full names and details. Islands in white are UNINVADED islands, islands in light grey are MANAGED islands, and islands in dark grey are INVADED islands. Burrow densities are indicated as follows: standard font: <0.05 burrows m^{-2}, bold font: 0.05 to 0.5 burrows m^{-2}, and italic font >0.5 burrows m^{-2}.

Fig. 2.2 Mean seedling density (#seedlings m^{-2}) by height category and rat history. Only the smallest seedlings (0–15 cm: $F_{1,2}$=4.67; P=0.02) showed significant differences between categories of rat status. Standard errors are shown.

Fig. 2.3. . Relationship between burrow density per plot (number of burrows m^{-2}) and maximum seedling density per plot (number of seedlings m^{-2}) at the within island scale ($F_{1,11}$=20.9, p=0.001). Maximum values for burrow classes (in increments of 5 except between 0.61 and 0.94 burrows which are all one class) are shown.

Fig. 2.4. Differences in woody seedling community characteristics associated with rat history including (a) seedling density (seedlings m^{-2}), species richness (# species m^{-2}) and diversity (H′) and (b) rarefaction results for plant species richness (H' not shown). Seedling density was greater on MANAGED islands (Fig. 2.3a: $F_{1,2}$=2.72, P=0.10) while both density ($F_{1,2}$=4.20, P=0.03) and diversity ($F_{1,2}$=10.3, P=0.001) were significantly lower on MANAGED islands. Standard errors are shown.


ISLAND
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INVADED
MANAGED
UNINVADED
0-0.05 seabird burrows
0.06-0.49 seabird burrows
≥0.50 seabird burrows
1.0
0.9
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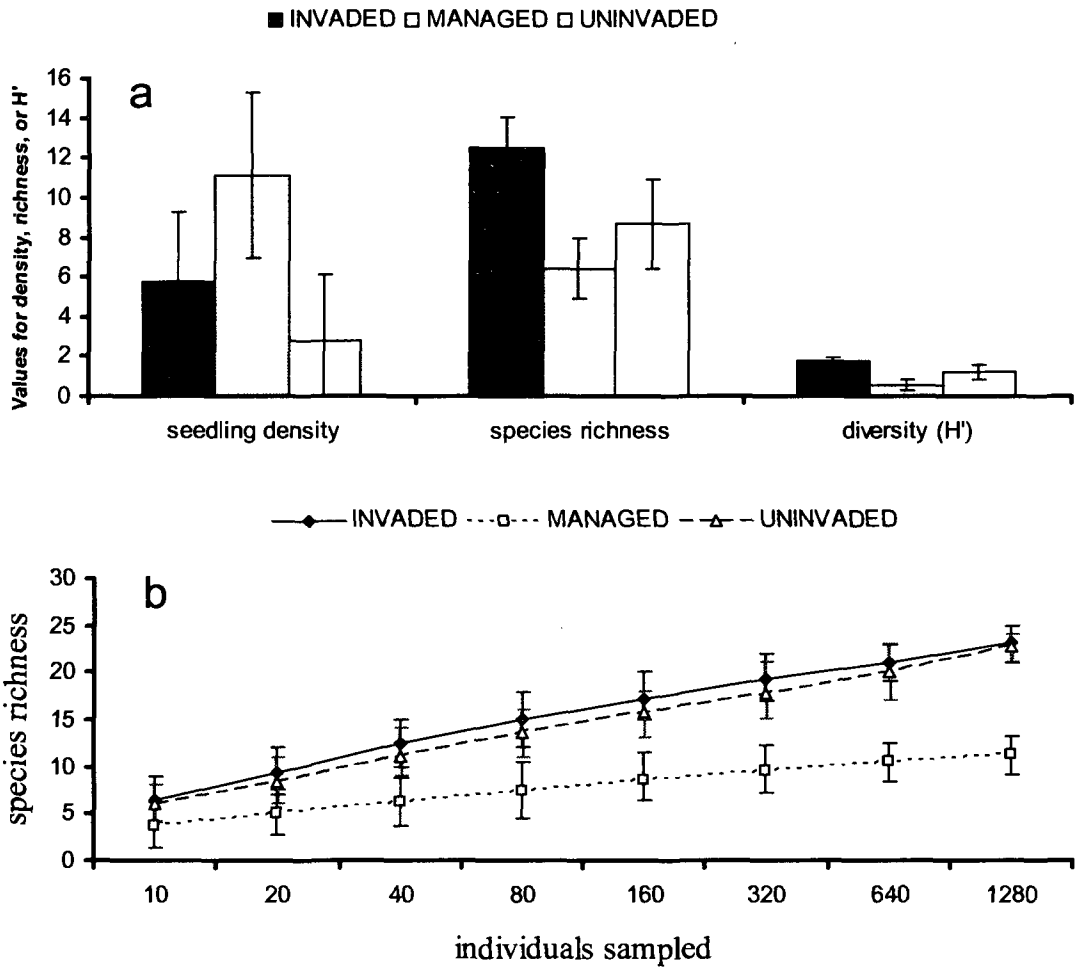
R- Squared

Figure 2.1


INVADED MANAGED UNINVADED
a
Values for density, richness, or H'
16
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12
10
8
6
4
2
0
seedling density
species richness
diversity (H')
INVADED MANAGED UNINVADED
b
species richness
30
25
20
15
10
5
0
10
20
40
80
160
320
640
1280
individuals sampled

Figure 2.4

CHAPTER 3:

INVASIVE RAT AND BURROWING SEABIRD EFFECTS ON SEEDS AND SEEDLINGS ON NEW ZEALAND ISLAND[1]

[1] Grant-Hoffman, M.N., C.P.H. Mulder, P. J. Bellingham (2009) Invasive rat and burrowing seabird effects on seeds and seedlings on New Zealand islands. Prepared for submission in *Oecologia*.

ABSTRACT

Rats (*Rattus rattus, R. norvegicus*) are transformational island important invaders. They alter vegetation indirectly through predation on burrowing seabirds. These seabirds affect vegetation through marine-derived nutrient inputs to land and via physical disturbance from trampling and burrowing. Rats also directly affect vegetation though consumption. Woody seedling species richness and density on northern New Zealand offshore islands are similar on islands with no history of rats and islands with current rat invasions. However, certain plant species decrease dramatically in abundance when rats invade. Conversely, seedling density increased on islands where rats have been eradicated or kept at low densities due to eradication attempts, and species richness and diversity declined. On these islands a few woody species have relatively high densities. We performed field experiments on offshore northern New Zealand islands along with laboratory and greenhouse experiments to determine the mechanisms driving these observed patterns in seedling communities. We found that seed and seedling density and richness decrease after rat invasion due to selective consumption of both seeds and seedlings. Plant species richness and density of seeds is higher in the presence of seabirds, possibly due to increased seed burial with seabird burrow formation. In addition, at very high seabird densities, potential seedling density and richness (based on seed germination rates) are high, but actual seedling density and richness are low due to extreme physical disturbance. Higher species richness at higher seabird burrow densities may be due in part to higher numbers of non-native species. Both invasive rats and burrowing seabirds can have large effects on seed and seedling communities on New Zealand islands.

INTRODUCTION

Invasive rats (*Rattus norvegicus, R. rattus*) have been introduced to more than 45 island groups worldwide (Atkinson 1985, Thorsen et al. 2000), and can have major impacts on plant populations and communities both directly through herbivory and indirectly through their impact on burrowing seabirds. Rats are major seabird predators (Drever and Harestad 1998, Major et al. 2007), and many burrowing seabirds do not coexist with rats (see review Jones et al. 2008). When rats extirpate seabird colonies they curtail allochthonous inputs of nutrients and end the disturbance regime seabirds impose. In addition, rats exert herbivorous pressures by selecting seeds and plant parts for consumption (Campbell 1978). Woody plant communities may be particularly vulnerable to the pressures of both burrowing seabirds (Maesako 1999) and invasive rats (Campbell 2002).

Plant recruitment, especially of tree and shrub species, can increase after rat eradication from islands (Allen et al. 1994, Campbell 2002, Grant-Hoffman et al. 2009). In addition, in exclosure studies and comparisons between areas with and without rats depression of plant recruitment has been attributed to rat herbivory (Campbell and Atkinson 1999, 2002). Many of these studies considered *R. exulans*, a smaller species than *R. rattus* or *R. norvegicus*. There are few studies, however, that use experimental manipulations to consider the effects of *R. rattus* and *R. norvegicus*. By using controlled experiments we can better isolate the mechanisms driving observed patterns.

Seabirds are abundant on many islands worldwide, where they are major drivers of ecosystem processes (Gillham 1956, Croll et al. 2005, Ellis 2005, Fukami et al. 2006).

Seabirds transport nutrients from sea to land, and their allochthonous inputs (guano, dead chicks, egg shells, and occasional dead adults) increase soil nitrogen, carbon, phosphorous, and acidity (Okazaki et al. 1993, Anderson and Polis 1999, Mulder and Keall 2001, Fukami et al. 2006, Roberts et al. 2007). These seabird inputs cascade through island systems affecting vegetation composition (see review Ellis 2005, Bancroft et al. 2005b) and productivity (see review Ellis 2005, Wait et al. 2005).

Seabirds also cause physical disturbance to island ecosystems. Seabirds, through trampling and burrowing, can bury seeds and litter, resulting in reduced litter aboveground (Fukami et al. 2006). In addition, increased variance in litter distribution can create a patchwork of microhabitats (personal observation). Physical disturbance can also prevent seedling establishment (Maesako 1999, Roberts et al. 2007) and alter plant species composition (see review Ellis 2005). Burrowing seabirds (order Procellariiformes: prions, petrels, and shearwaters) can change soil physical properties, for example by increasing soil penetrability and the range of soil surface temperatures (Bancroft et al. 2005a). Seabird colonies can act as disturbance patches in the landscape, increasing species richness (Archer et al. 1987) and the probability of plant invasion (Mulder et al. 2008). However, at very high burrow densities some plants may not be able to survive the severe disturbance regime (Vidal et al. 2000).

Previously, we compared woody seedling communities in secondary forests on 22 northern New Zealand islands with different histories of invasion by *R. rattus* or *R. norvegicus* (Grant-Hoffman et al. 2009). Islands with no history of rats and islands with current rat invasions had similar seedling densities and seedling species richness and

diversity. Islands from which rats had been eradicated had higher seedling densities but lower seedling species richness and diversity and were dominated by a few woody species (Grant-Hoffman et al. 2009). Here we examine the mechanisms through which invasive rats and burrowing seabirds affect plant regeneration. We collected observational data and performed experiments on several islands, in the greenhouse, and in the laboratory to test which mechanisms were driving the observed patterns in the woody seedling community.

We first sought to understand how invasive rats and burrowing seabirds were affecting the seed community. We asked the following questions:

1) Are rats reducing density or species richness of seeds in the litter and soil? We hypothesized that species richness of seeds and density in the litter and soil seedbank is reduced by rat consumption (Fig. 3.1; boxes *a, b*). Rats may also act as seed dispersers, but this would be limited to certain species and could be less common than consumption (Fig. 3.1; boxes *a*, *b*).

2) Is increased seabird burrow density associated with increased density and richness of seeds in the litter and soil? Seabirds reduce litter, but this is a non-selective process. Unlike for rats, we did not expect the percentage of litter (by weight, g) that was reproductive material (seeds, fruits, flowers, pieces of seed or fruits) to be reduced by the presence of seabirds (Fig. 3.1; box *c*). Similarly, the number of seeds in the soil seed bank was not expected to be reduced by seabirds, and germination may be increased due to

burial by seabirds or higher nutrient availability for plant reproduction in the presence of seabirds (Fig. 3.1; box *c*).

Next, we examined how invasive rats and burrowing seabirds affect the seedling community. We asked the following questions:

3) Does rat consumption decrease seedling density and richness? We hypothesized that both seedling density and richness would increase when seedling communities were protected from the selective herbivory by rats.

4) Does the physical disturbance of seabirds decrease seedling density or alter seedling species richness? We hypothesized that microsite changes (increased light and nutrient additions; Mulder et al. 2008) would provide good germination and growth conditions for seedlings, but that the physical disturbance by seabirds would damage seedlings and limit seedling germination and growth (Fig. 3.1; boxes *c, d, e*). In addition, since the physical disturbance by seabirds is not a highly selective process, we expected there to be fewer changes in species richness than in seedling density.

By beginning to understand the mechanisms that are driving the patterns seen in seed and seedling communities, scientists and managers can concentrate their efforts on species and processes most affected by rat invasions.

METHODS

Study Area

We established and sampled four 100 m^2 plots on seven islands (Middle, Raumahuanui, Whenuakura, Te Haupa, Hauturu, Motueka, Motutapere) in warm temperate northern New Zealand from January to May in 2005 and 2006 (Table 3.1). These islands were chosen (from a total pool of 22 for which we had previous information, Fukami et al. 2006, Grant-Hoffman et al. 2009), for ease of access (necessary for repeated visits), and their known rat status. All are of volcanic origin except Te Haupa (sedimentary origin) and range in size from 3 to 46 ha. They are all within 20 km of the mainland and have a history of anthropogenic disturbance (fire, and some previously farmed). All are covered with secondary forest and have or had populations of burrowing seabirds (Procellariiformes; Holdaway 1999, Worthy and Holdaway 2002). We placed two of the 100m^2 plots were placed in areas of higher burrow densities and two in areas with lower burrow densities. Plots were placed in mature forest when burrow densities were consistently high or consistently low across an island. Previous research has shown that islands with no rats, and therefore high numbers of seabirds, have higher soil carbon, nitrogen and phosphorous and lower soil pH than island with rats and lower numbers of seabirds (Fukami et al. 2006, Table 3.2).

We used WaxTags (Pest Control Research Ltd., New Zealand) to confirm rodent presence. WaxTags were placed low on two trees haphazardly located within each plot to determine if rats were present in the area. These tags show teeth marks when they are investigated by rodents and are meant to show presence only, not density. Any neophobia

that rodents may have had should have been overcome in the one year that the tags were left in place. In addition we performed feeding trials with *R. norvegicus* on one island (Pakihi). This island was chosen because it could be accessed easily, our ability to stay on the island for an extended period, as well as documented activity of *R. norvegicus*. This island has pastureland, on which cattle graze and secondary forest (Table 3.1). Middle and Ruamahuanui Islands have no history of rodent invasion and have large populations of burrowing seabirds (Table 3.1). Whenuakura Island had *Rattus norvegicus* that were eradicated in 1985. This island also has a population of grey-faced petrels (*Pterodroma macroptera*), which were never extirpated by the rats. Te Haupa and Hauturu Islands both had invasions of *R. norvegicus* that were eradicated in 1989 and 1985, respectively. However, these islands also have current mouse (*Mus musculus*) invasions that were previously masked by the presence of *R. norvegicus*. Finally, despite an eradication attempt in 1996, Motutapere Island has a current population of *R. rattus* (Table 3.1). We used an additional fifteen islands (total 22) with 2 to 4 plots per island for litter collections.

Changes to the seed community

Germination trials

We used germination trials to test for the impacts of seabird and rat activity on seed incorporation into the seed bank (Fig. 3.1; boxes *b, c*). One soil core (50 mm diameter) was collected from the approximate center of each plot. Soil was separated into 3 depths (0-59 mm, 60-120 mm, and 130-200 mm) to determine if seabird activity has

resulted in deep burial of seeds. Depths were chosen for ease of collection and to reflect depths which may be disturbed by seabird burrowing activity. From each soil depth we used the same volume (980 mm^3) of each soil sample for germination trials. Soils were placed in plastic bags and kept cool until germination trials were started. Soils (3 depths per plot * 4 plots per island * 6 islands = 72 samples) were placed in pots in a greenhouse on 17 March 2006, and emerging plants were counted weekly and identified to species. The experiment was terminated on December 1, 2006 due to declined emergence rates and high liverwort and moss growth.

Seed traps

We used seed traps to test for the impact of rat consumption on seeds present in seed rain and to compare this to seeds found in the litter and soil seed banks (Fig. 3.1: box *a*). Seed traps were constructed of plastic boxes (13 cm by 17 cm), shade cloth, and bird mesh (Fig. 3.2b). These traps were not considered 'rat proof', but were expected to deter rats for the 8 week duration of the experiment. Seven seed traps were placed in a stratified random design within each plot (4 plots * 6 islands = 168 seed traps) in February and March of 2005. The traps were emptied approximately 8 weeks later and again between February and March 2006 when they were removed from the islands. After the 8 week trial, they showed no signs of disturbance by rats or birds (bird mesh intact). Due to signs of disturbance (torn bird mesh) in many of the traps when removed at the end of the year, we used data from the 8 week trial only. All seed material was

counted and identified to species when possible (Poole and Adams 1964, Salmon 1986, Webb and Simpson 2001).

Reproductive material in the litter

We evaluated post-dispersal seed availability by examining seeds and reproductive material in litter samples (Fig. 3.1; boxes *b, c*). For this data set only we used 22 islands (Grant-Hoffman et al. 2009). Seven litter samples were collected from each plot in a stratified random design. A sample consisted of all material on the surface of the soil within a 0.01 m^2 area. All reproductive material, including seeds, seed coats, fruits, and flowers, was removed from each sample and identified with help of a magnifying glass using Webb and Simpson (2001) as the primary reference. Both the reproductive material and remaining sample material were dried for 48 hrs at 60°C and weighed.

Feeding trials

We evaluated rat preferences for seeds of seven woody plant species (Fig. 3.1; boxes *a, b*). We placed seed with similar biomass (based on seed size) into covered trays (Fig. 3.2c). The covers were meant to deter avian consumption. Ten trays were placed in areas around the island of Pakihi (Table 3.1) on 18 February 2006 to allow the animals to get accustomed to them. Feeding trails began on 10 March 2006. We used seeds, seed capsules, or fruits depending on what would be available to the rats in the wild. We chose species that we could collect easily and included both a variety of sizes and species that

we expected to be eaten, as well as some species we expected to be avoided. Species and number of fruits used were: *Coprosma macrocarpa* (50 fruits), *Pittosporum crassifolium* (5 seed capsules), *Pseudopanax lessonii* or *P. chathamicus* (75 seed capsules), *Hedycayra arborea* (25 fruits), *Streblus banksii* (85 fruits), *Melicope ternata* (30 seeds), and *Dysoxylum spectabile* (5 seed capsules). Each station housed 4 plant species, and (due to limited availability of some species) each species was used in at least 3 stations. *Coprosma macrocarpa* and *Pittosporum crassifolium* were used in all stations. All seeds were left out for five nights. Each morning we observed and counted any remaining seeds. We also noted any signs of rats (chewed seeds, rat droppings, footprints). After five nights we counted any remaining material and collected traps and remaining plant material.

Viability tests for Pittosporum crassifolium

We tested *Pittosporum crassifolium* seeds for viability after they were consumed by *Rattus norvegicus* (Fig. 3.1; *a, b*). Seeds of this species are readily eaten in the field, but the seedling population recovers well after rat eradication (Grant-Hoffman et al. 2009). Therefore, it is possible that this species is dispersed by rats. We housed five laboratory-raised brown Norway rats in animal quarters at the University of Alaska Fairbanks (UAF). Rats were housed in a laboratory setting under Assurance #06-02 from the UAF Institutional Animal Care and Use Committee (IACUC) and Permit # 08-057 from the Alaska Deptartment of Fish and Game. We first exposed rats to unflavored gelatin mixed with peanut butter to encourage consumption of a new food source (gelatin

mixture). Rat chow and water were available *ad libitum*. We then added 20 to 30 seeds of *Pittosporum crassifolium* to the flavorless gelatin matrix. This mix was offered to subjects for 12 hours (8 pm to 8 am). Four of the five rats consumed all the seeds and gelatin. After 48 hours the cages were cleaned and all excrement was collected and examined for seeds. For all four subjects that consumed seeds we found seeds within excrement. Seeds appeared to be intact upon examination with a stereo microscope. These seeds were stored for two weeks in a refrigerator, then placed in a potting mix in the greenhouse for 90 days and kept moist to assess germination. We also placed control seeds not eaten by rats in the same potting mix and left them out for 90 days to determine germination.

Changes to the seedling community

Exclosure experiment

We used exclosures to test for the impact of seabird and rat activity on seedling loss between the seed bank and germination stage and on short-term seedling survival (Fig. 3.1; *d, e*). Exclosures were constructed of wire mesh (20 mm) and plastic piping and were approximately 0.32 m^2 in area (Fig. 3.2a). Exclosures were designed to exclude both seabirds (*Pterodroma macroptera, Pelacanoides urinatrix, Puffinus carneipes*) and rats (*Rattus norvegicus, R. rattus*), but the mesh was not sufficiently small to exclude mice. Within each 100m^2 plot we randomly placed two exclosures along with one exclosure control, to account for unintended effects of exclosures (Fig. 3.2a), and one unmodified control subplot marked with flagging tape (4 plots per 6 islands = 48

exclosures and 48 control areas). Exclosure controls were used to test for any unintended effects of the exclosure structure (e.g., increased shading or litter collection). Exclosures were placed on islands in February and March of 2005 and left in place for one year. Seedlings were counted and identified to species when the structures were set out in February and March 2005, approximately 8 weeks later in April 2005, and approximately one year later in February and March 2006. We placed a WaxTag (Pest Control Research Ltd., New Zealand) within each exclosure to determine if rats were entering the exclosures. All WaxTags were collected along with exclosures in February and March 2006.

Statistical Analyses

The original design of our study was conducted over two years, incorporated three levels of rat status: two islands never invaded, two islands with current infestations of rats (*Rattus rattus* or *R. norvegicus*), and two islands where rats had been eradicated. However, after the first year of our study we found evidence of mice from chew tags on both Te Haupa and Hauturu, and this discovery changed our design. Rats were successfully eradicated from Te Haupa in 1989. A rat eradication attempt on Hauturu in 1985 was thought to have failed; however, we found no evidence of rats on Hauturu, and populations were likely low if rats were present. We presume that the mice had been present on these islands prior to rat eradication, but had remained undetected due to suppression by rat populations (Innes et al. 1995). Therefore, our new design was: two islands with no history of invasive rats, two islands where rats had been eradicated but

with mice infestations, one island with a current rat infestation, and one island where rats had been successfully eradicated and no other rodents were found. In the second year of our study we were able to replace Hauturu with Motutapere (an island with a confirmed current rat infestation) returning us to our original design. Therefore, our germination trials follow our original design. For exclosure and seed trap trials, both of which ran for two years, we ran several separate ANOVAs, grouping the two islands with no history of rats together and the two islands with a history of rats and current mice invasions together. The remaining islands were analyzed separately. We did not attempt to keep our original design since mice also consume seeds (e.g., Ruscoe et al. 2005) and since herbivory by mice may overlap with that of rats. All analyses were performed in SAS (SAS Institute 2002).

Germination trials

We used a split plot design to analyze seeds in the seedbank at the island scale, using islands as the unit of analysis. We considered the effects of rat status and depth of sample on species richness of seedlings germinating, seedling density (representing the total number of seeds that germinated), and percent of germinating seedlings that were non-native seedlings. The block level consisted of islands grouped by latitude with three islands in each of two blocks. Plot level treatment was rodent status with three levels (rat invaded islands, uninvaded islands, and rat eradicated islands). Sub-plot level was the depth from which the soil was collected. We ran additional separate ANOVAs for the two islands with no history of rats, for the two islands with current rat invasions, and for

the two islands where rats had been eradicated to consider burrow density effects at the within island scale. Plots were the unit of analysis at this scale. We blocked by island and included burrow density as a continuous variable (log_{10} scale) and depth as a categorical treatment. We also considered a burrow by depth interaction.

Seed traps

We used separate ANOVAs for the two islands with no history of rats, for the one island with a current rat invasion, for the one island where rats had been eradicated and mice were not present, and for the two islands with mice to consider the effects of rodents and seabird burrow density on species richness and number of seeds found in seed traps. We blocked by island, where appropriate, and included burrow density as a continuous variable (log_{10} scale).

Reproductive material in the litter

We used a mixed model to examine the relationship between both species richness and amount of material (total weight and weight as a percentage of the total) in the seed community, and rat status and burrow density (log_{10} scale). Since the presence of rats was always associated with low seabird density, these two variables were confounded. We therefore performed analyses at two scales: within islands and among islands. Plots were the unit of analysis at the within-island scale assesing seabird effects. Response variables were averaged per plot (7 samples per plot) and with island as a blocking variable. Islands were the unit of analysis at the between-island scale to test for rat effects. At this

scale response variables were averaged per island with island size as a covariate to account for variation due to the island size (MacArthur and Wilson 1967).

Feeding trials

We calculated the percent of plant material of each species removed from the six stations that were visited by rats. We used totals for the entire five night period. We attributed seed removal to rats based on signs such as chewed seeds, feces, or footprints.

Exclosure experiment

As we did in our seed trap trials we ran separate ANOVAs for islands with different rodent histories. We considered the effects of rat status, burrow density, and their exclusion on seedling density, species richness, and percent of seedlings that were non-native species.We included island as a blocking variable where appropriate, burrow was included as a continuous variable ($\log_{10}$ scale), and exclosure was included as a fixed factor.

RESULTS

Changes to the seed community

Germination trials

At the island scale neither rat status ($P>0.2$; Table 3.3) nor soil depth ($P>0.1$; Table 3.3) had significant impacts on seedling density, species richness, or percent non-native species.

At the within island scale on the uninvaded islands, Middle and Ruamahuanui, seedling density increased with increasing burrow density ($F_{1,17}=4.36$, $P=0.05$; Fig. 3.3a). In addition, more seedlings germinated from the shallowest depth (depth 1) than from the deepest depth (depth 3) ($F_{2,17}=5.15$, $P=0.02$; contrasts, $P=0.01$). The middle depth was not statistically different from either the shallowest or deepest depth (contrasts, $P>0.2$; Fig. 3.3a). Seedling density showed only a marginal increase with increasing burrow density on invaded islands ($F_{1,17}=3.46$, $P=0.08$) and was not significant on eradicated islands ($P>0.6$). Depth was not significantly related to seedling density on either invaded ($P>0.1$) or eradicated ($P>0.8$) islands.

Similarly, species richness on the uninvaded islands increased with increasing burrow density ($F_{1,17}=5.40$, $P=0.03$). Also, more species were found at the shallowest depth than at either of the deeper soil depths ($F_{2,17}=4.82$, $P=0.02$; contrasts, $P=0.04$ for both; Fig. 3.3b). However, the lower two depths were not different ($p>0.9$). Again, species richness of seedlings was not related to burrow density or depth of sample on either invaded or eradicated islands ($p>0.1$).

We found only a marginal increase in the percentage of non-native species with increasing burrow density on uninvaded islands ($F_{1,17}$=3.34, P=0.08). No other islands showed significant trends.

Seed traps

There were no significant relationships between species richness or density of seeds found in seed traps and density of seabird burrows in the analyses on islands with no history of rodent invasions (P>0.19); the analysis on the island with a current rat invasion (P>0.31); the analyses of islands where rats had been eradicated and mice were present (P>0.1); or the analyses of the island where rats had been eradicated and mice were not present (P>0.17).

Reproductive material in the litter

Both the total weight of reproductive material and the percentage of the litter that was reproductive material decreased with increasing burrow density when comparing plots within islands (total weight $F_{1,28}$=9.94, P=0.004; percentage weight $F_{1,28}$=7.81, P=0.01). However, for both total weight of reproductive material and percentage of the litter that was reproductive material, relationships were determined by plots on Middle island. Middle island has no history of rat invasions and very high seabird burrow densities, which had relatively high amounts of reproductive material (Fig. 3.4a). When this island was excluded from analyses the relationship was no longer significant (Middle Island - total weight $F_{1,1}$=14907, P=0.005; percent reproductive material $F_{1,1}$=688,

P=0.02; All other islands – total weight $F_{1,25}$=1.39, P=0.2; percent reproductive material $F_{1,25}$=0.12, P=0.73).

Species richness was not related to burrow density within islands (P=0.5). However, when comparing islands, uninvaded islands had higher species richness in the litter than invaded islands ($F_{2,16}$=6.47, P=0.009; contrasts P=0.01 for both). However total weight of reproductive material and percentage of the total litter weight that was reproductive material was not significantly related to either burrow density or rat status among islands (P>0.1).

Feeding trials

Rats visited six of ten feeding stations over the five-night trial, as inferred from fruit damage, footprints, and feces; our reported results are from these six stations. Seed and fruits fell into two categories: those that were frequently eaten (more than 20% removal from feeding stations) and those that were rarely eaten (less than 7% removal from feeding stations). Four of the seven fruits tested were rarely eaten: *Hedycarya arborea, Pseudopanax spp., Dysoxylum spectabile, and Melicope ternata*. The remaining three species were frequently eaten and showed substantial removal of fruits (*Pittosporum crassifolium* 86.6%, *Coprosma macrocarpa* 23.4%, and *Streblus banksii* 45.3%). One of these, *Streblus banksii*, was apparently consumed by an unidentified invertebrate within 48 hours, afterwords none of the stations with this species was visited by rats.

Viability tests for Pittosporum crassifolium

Seeds of *Pittosporum crassifolium* are able to pass through digestion in *Rattus norvegicus* unharmed, as determined by visual observation. While these seeds did not germinate when placed in the greenhouse for 90 days, we also had no germination among control seeds (that had not passed through rat digestion).

Changes to the seedling community

Exclosure experiment

We found no evidence from WaxTags of rats on any islands except for Motueka. The WaxTags on Motueka were not disturbed inside exclosures. WaxTags on Te Haupa and Hauturu showed evidence of mice both inside and outside exclousres.

Seedling density and species richness of seedlings increased with increasing burrow density (seedling density $F_{1,27}$= 9.55, P=0.0003; species richness $F_{1,27}$=53.22, P<0.0001; Fig. 5a, b) and inside exclosures (seedling density $F_{1,27}$=9.55, P=0.005; species richness $F_{1,27}$=38.77, P<0.0001; Figure 5a, b) on the two uninvaded islands. Seedling density and species richness was also higher inside exclosures on the island with a current *Rattus rattus* invasion (seedling density $F_{1,12}$=8.11, P=0.005; species richness $F_{1,12}$=11.76, P=0.01; Fig. 3.6a, b).

Only seedling density was higher inside of exclosures on the two islands where we found mice (mean ± SEM: inside exclosures =33.4 ± 8.01; controls =10.2 ± 2.45; $F_{1,27}$=11.30, P=0.002) although these differences were not as large as on other islands. The proportion of the total seedlings found inside of exclosures on mice infested islands

was 76% compared to 91% for islands with no history of rodent invasion, 88% for the rat infested island, and 88% for the island where rats had been eradicated and seabirds were still present. In contrast, on the island where rats had been eradicated and no rodents were present, only species richness was higher inside of exclosures (mean inside exclosures =2.5, SD=0.92; mean in controls =0.87, SD=0.83; $F_{1,12}$=13.20, P=0.003).

The percent of seedlings that were non-native was marginally more abundant within exclosures on uninvaded islands ($F_{1,27}$=2.82, P=0.10). The most common non-native species was *Phytolacca octandra*. We did not find non-native species in sampled exclosure areas on any of the other islands studied.

DISCUSSION

Changes to the seed community

Consumption by rats (Fig. 3.1; boxes a,b)

Rats consumed seeds contributing to lower densities and richness of seeds in the litter and seedbank on islands where rats have invaded. In feeding trails, seeds from three of seven species tested were consumed at high rates. This is consistent with numerous studies that have shown rat consumption of seeds of certain plant species (see review Grant-Hoffman and Barboza 2009). In addition, we found low species richness of reproductive material in the litter on islands where rats were or had been present. We also found an increase in seedling germination inside exclosures on the island that currently had rats, although we could not distinguish between consumption of seedlings and consumption of seeds. In addition to low species richness in general, prolonged selective consumption by rats may cause an absence of some species of seeds on islands with a history of rat invasion. As an example we found no seeds or seedlings of *Streblus banksii* where rats were or had been present.

We found that *Pittosporum crassifolium* seeds are consumed by rats, but we know that seedling density of this species recovers once rats are removed (Grant-Hoffman et al. 2009). We found via visual observation that this species can pass through *Rattus norvegicus* digestion visually unharmed. Thus, this species may be dispersed by rats, which may explain its ability to recover after rat eradications. It is still unclear how this species is surpressed by rats, but it may be vulnerable at a different life stage (Campbell and Atkinson 2002).

Physical and chemical effects of seabirds (Fig. 3.1; box c)

Seabirds reduced seed density in the litter while increasing the density of seeds in the soil seedbank, which may be a result of seed burial during burrow formation. In addition, soils from areas with high burrow density yielded greater seedling germination in the greenhouse. High seedling germination from soils taken from seabird colonies or when seabirds are excluded has been found on other islands (Bancroft et al. 2005b, Roberts et al. 2007). In addition to increased seedling germination, on the 12 islands with substantial seabird colonies, we found lower amounts of reproductive material in the litter at higher burrow densities. This may be another indication of incorporation of this material, along with litter, into the soil with burrow formation at higher burrow densities. High germination in soils from areas of high burrow density may result from increased seed production, or higher germination rates. However, we were unable to evaluate the effects of burrow density on seed production due to the short duration of and high variation among our seed trap trials. By incorporating seeds into the soil seedbank seabirds may be allowing for increased seed germination. Seeds may easily dry on the surface of the soil with little or no litter for cover on seabird colonies (Maesako 1999), and burial may increase germination rates.

While species richness of seeds and reproductive material was greater with seabird presence, this effect was likely driven by rats and not seabirds. Uninvaded islands had higher species richness of reproductive material found in the litter than did islands with a history of rats. However, these increases may be a result of an absence of rat consumption, and not an increase due to seabird presence or density. In addition, on

uninvaded islands species richness of seedlings germinating from collected soils increased with increasing burrow density. In contrast, observations in the field from our study sites indicate that seedling species richness at very high burrow densities is low (Grant-Hoffman et al. 2009, Mulder et al. 2008). However, this decrease appears to be the result of low observed seedlings due to physical disturbance, not to low species richness of germinating seedlings. In general, other studies have also found that plant species richness decreases with increasing burrow density (Ellis 2005).

Changes to seedling community

Physical and chemical effects of seabirds (Fig. 3.1; boxes d,e)

Seabirds appear to increase the density of seeds in the soil seedbank and germinating seedlings, but seabird physical disturbance reduces seedling density. We found much higher seedling density inside exclosures versus outside of them on uninvaded islands. This has also been found on other islands (Roberts et al. 2007). Seabirds may also influence seedling growth and survival by changing the chemical environment (Bancroft et al. 2005b). Common plant species *Entelea arborescens* (Tiliaceae), *Corynocarpus laevigatus* (Corynocarpaceae), and *Streblus banksii* (Moraceae) showed significantly increased biomass when grown in soils from islands with active seabird colonies and no history of rats (Fukami et al. 2006). High numbers of germinating seedlings inside exclosures in high seabird density areas may also be due to more plentiful seeds in the soil. However, on an active seabird colony, the number of

seedlings is restricted due to extreme physical disturbance from burrowing activities (Maesako 1999).

Greater seedling species richness inside exclosures and at higher burrow densities on uninvaded islands indicate that overall plant species richness may be higher in the presence of seabirds, even though it may be depressed at actual nesting sites when burrow densities are high. Seabirds likely influence species composition by increasing physical heterogeneity through burrowing, nest building, and landing. They may also increase light levels. Disturbances thereby may promote greater plant species diversity (Connell 1978). In addition, apart from general increases in nutrients in the soil (see review Ellis 2005), increases in the spatial heterogeneity of the soil chemical composition on seabird colonies have been found in other areas (Wait et al. 2005) and may also contribute to higher species richness at higher burrow densities.

Consumption by rats (Fig. 3.1; boxes a,b,e)

In addition to consuming seeds, rats also consume seedlings, as evidenced by increased seedling density inside exclosures on the rat invaded island. Several other studies have documented rats eating seedlings (see review Grant-Hoffman and Barboza 2009). There were also significantly higher seedling densities inside of exclosures on mice infested islands. However, these increases were not as pronounced as those on islands with substantial populations of seabirds or current rat infestations. Exclosures may have reduced but not eliminated mouse access leading to the observed intermediate impact on density.

Non-native species

Greater species richness at higher burrow densities may be due in part to increased numbers of non-native species. While we did not find a significant increase in non-native species with increased burrow density, we found only non-native species in our exclosure trials on uninvaded islands. This may be due to chance. However, other studies have found increased non-native plants on seabird colonies (Bancroft et al. 2005b). At high burrow densities, observed non-native plant species may be kept at a minimum due to the physical pressure of burrowing and trampling. However, through rapid growth and reproduction, these plants may be able to maintain a significant presence in the seedbank. Plants with a short juvenile period and an ability to reproduce quickly can have rapid population growth and are more likely to be invasive (see review Rejmanek and Richardson 1996). On seabird colonies, species with these characteristics are able to take advantage of short periods of low activity (non-breeding times), or small areas of low disturbance (through chance) to quickly grow and reproduce (Gillham 1956). When high levels of disturbance associated with high burrow densities are removed, native plants may lose their advantage allowing quick growing and reproducing non-native plants to take advantage of the abundant resources and overtake native species. Reductions in seabird populations will likely have negative effects on native plants which rely on this disturbance regime (Ellis 2005). If birds are removed from the system a flush of non-native species may occur, as seabird colonies may provide an access point for non-native plant species.

CONCLUSIONS

When rats invade islands they consume seeds and seedlings and reduce species richness of reproductive material and germinating seedlings, potentially altering the plant community. In addition to consuming seeds, rats extirpate burrowing seabirds that can also have marked effects on seed and seedling communities. Species richness of seeds and germinating seedlings is high on seabird colonies, although physical disturbance by seabirds kept both observed species richness and density of seedling communities low. Some of this increased richness in the seedbank may be due to an increase in non-native species. However, adult non-native species may be repressed by physical disturbance when seabirds are present.

When rats invade, plant communities are faced with the introduction of an herbivore that is able to change plant communities through direct consumption. However, rats also remove burrowing seabirds, an integral part of the system. In order for managers to restore plant populations the legacy of rat consumption must be dealt with as well as restoring burrowing seabirds and the ecosystem processes that these birds influence.

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Table 3.1 – Information on islands used for experiments. Pakihi Island was used for feeding trials only.

Island	Latitude (°S)	Longitude (°E)	Area (ha)	Distance from mainland (km)	Rat History	Seabirds present	Seabird density (burrows m^{-2}) mean	Seabird density (burrows m^{-2}) range
Ruamahaunui	36.95	176.09	32.4	19.9	Uninvaded	*Pterodroma macroptera*	0.14	0.02-0.35
Middle (Atiu)	36.6	175.84	13.5	8.3	Uninvaded	Pelacanoides urinatrix, Puffinus carneipes	0.52	0.02-0.98
Motutapere	36.78	175.40	45.6	2.5	*Rattus rattus* eradicated 1996, reinvaded	none	0	---
Motueka	36.82	175.80	6.2	1.2	*Rattus rattus* or *R. norvegicus*	*Pterodroma macroptera*	0.03	0-0.06
Te Haupa	36.51	174.74	6.0	10.5	*Rattus norvegicus* eradicated 1989, *Mus musculus*	none	0	0-0.01
Hauturu	37.21	175.89	10.3	0.5	*Rattus norvegicus* eradicated 1985?, possible low population, *Mus musculus*	*Pterodroma macroptera*	0	---
Whenuakura	37.22	175.89	3.0	0.9	*Rattus norvegicus* eradicated 1985	*Pterodroma macroptera*	0.15	0.04-0.29
Pakihi	36.54	175.10	110.0	1.4	Rattus norvegicus	none	0	---

Table 3.2 – From Fukami et al. 2005. Effect of rat invasion, soil depth and their interaction on soil nutrients and pH. Mean values ± SEM are presented for rat-free and rat-invaded islands (n ¼ 9 islands for each island status). The ratios of mineral N to total N and of Olsen P to total P provide measures of the ratio of labile forms of N and P relative to total N and P. F values (with P-values in parentheses) from two-way ANOVA are presented for effects of island status (rat-free or rat-invaded), soil depth (0–10, 10–20, or 20–30 cm), and two-way interaction. Analyses were done on log-transformed data, except for d15N and pH. *Statistically significant values ($P < 0.05$).

	Island status			Soil depth	Island status * Soil depth
	Rat-free (UNINVADED)	Rat-invaded (INVADED)	*F* and *P* values	*F* and *P* values	*F* and *P* values
Total C (%)	9.88 ± 1.67	5.27 ± 0.69	28.47 (< 0.001)*	15.85 (< 0.001)*	0.94 (0.396)
Total N (%)	0.78 ± 0.10	0.43 ± 0.05	35.94 (< 0.001)*	17.87 (< 0.001)*	0.71 (0.496)
Total P (%)	0.30 ± 0.09	0.13 ± 0.04	6.77 (0.012)*	* 0.69 (0.507)	0.05 (0.954)
Mineral N/ total N (%)	12.67 ± 3.50	5.88 ± 1.16	15.16 (< 0.001)*	1.11 (0.339)	0.29 (0.749)
Olsen P/ total P (%)	6.92 ± 1.31	3.88 ± 0.90	13.40 (0.001)*	0.04 (0.964)	0.02 (0.982)
$\delta^{15}N$ (‰)	14.13 ± 0.62	10.87 ± 0.97	20.85 (< 0.001)*	2.82 (0.070)	1.16 (0.321)
pH	4.85 ± 0.21	6.63 ± 0.15	45.72 (< 0.001)*	0.24 (0.791)	*0.29 (0.749)

Table 3.3 – ANOVA results for the germination trials at the island scale. RS * SD represents rat status by soil depth interaction.

Factor	Degrees of Freedom	Seedling density		Species richness		% Non-native species	
		F	P	F	P	F	P
Rat status	2,2	1.40	0.42	2.32	0.30	3.11	0.24
Soil depth	2,2	5.49	0.15	11.24	0.08	0.10	0.91
RS * SD	4,4	1.08	0.47	0.93	0.53	2.13	0.24

FIGURE LEGENDS

Figure 3.1 – Diagram of a woody plant reproductive cycle with some potential effects of invasive rats and burrowing seabirds included. Lettered boxes refer to mechanisms addressed.

Figure 3.2 - (a) An exclosure plot (left) and exclosure control plot (right) on Middle Island, (b) Seed trap on Hauturu Island, and (c) Feeding trial exclosure with seeds inside on Pakihi Island.

Figure 3.3 – (a) Seedling density and (b) species richness by burrow density (log_{10} scale) for germination trials on uninvaded islands, Middle and Ruamahaunui. Soil sample depths are as follows: depth 1 = 0-59 mm, depth 2 = 60-129 mm, depth 3 = 130-200 mm for germination trials. Different letters indicate a significant difference between soil depths ($p<0.05$). Both seedling density ($F_{1,17}=4.36$, $P=0.05$) and species richness ($F_{1,17}=5.40$, $P=0.03$) also showed significant increases with increasing burrow density.

Figure 3.4 – (a) Percentage of the total litter weight represented by reproductive material, showing a significant decrease in reproductive material with increasing burrow density on a log_{10} scale ($F_{1,28}=7.81$, $P=0.01$). Middle island showed unusually high values. (b)Relationship between species richness of seeds found in the litter and burrow density among all islands (22 islands, $F_{2,26}=6.47$, $P=0.009$). Species richness decreased with increasing burrow density on log_{10} scale, but was highest on islands with no history of rats.

Figure 3.5 – (a) Seedling density and (b) species richness by burrow density (log_{10} scale) for the exclosure experiment on uninvaded islands, Middle and Ruamahaunui. Different letters indicate a significant difference inside (exclosure) and outside (control) of exclosures ($p<0.05$). Both seedling density ($F_{1,27}=9.55$, $P=0.0003$) and species richness ($F_{1,27}=53.22$, $P<0.0001$) also showed significant increases with increasing burrow density.

Figure 3.6 - Means ± SE for (a) seedling density and (b) species richness inside (exclosure) and outside (control) of exclosures for the rat invaded island, Motueka. Values are means from sample areas (0.32 m^2).

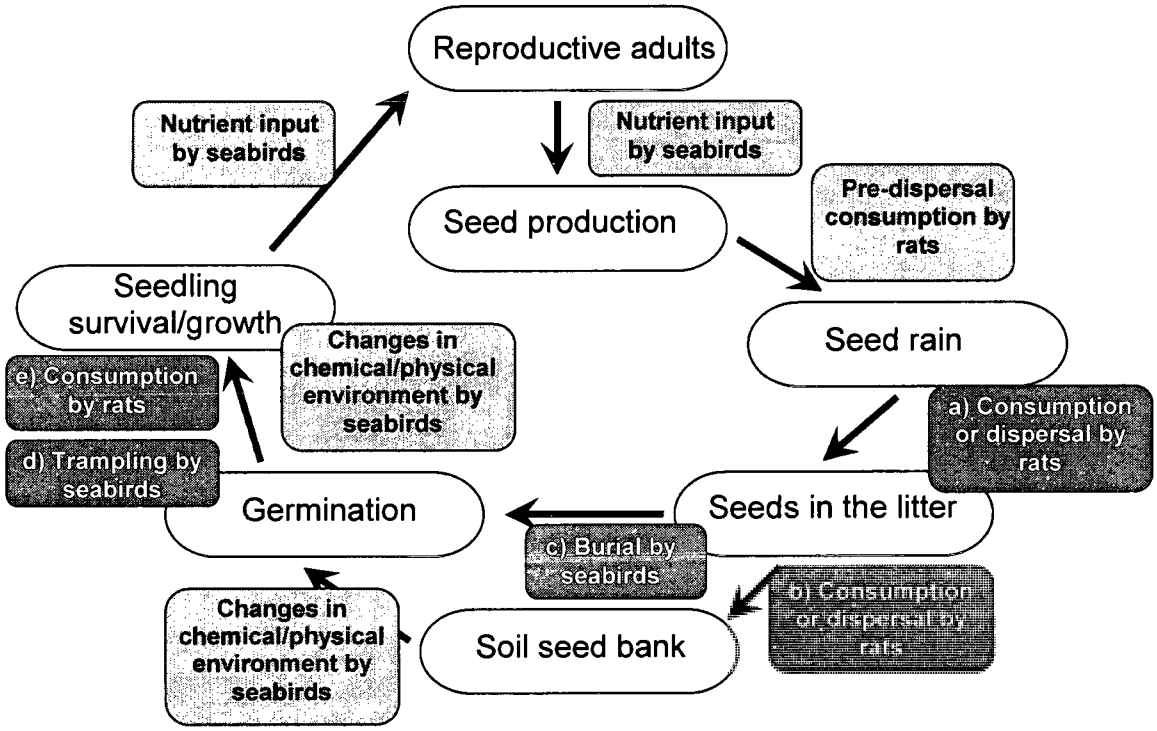

Reproductive adults
Nutrient input by seabirds
Nutrient input by seabirds
Seed production
Pre-dispersal consumption by rats
Seedling survival/growth
Changes in chemical/physical environment by seabirds
Seed rain
e) Consumption by rats
a) Consumption or dispersal by rats
d) Trampling by seabirds
Germination
Seeds in the litter
c) Burial by seabirds
b) Consumption or dispersal by rats
Changes in chemical/physical environment by seabirds
Soil seed bank

Figure 3.1

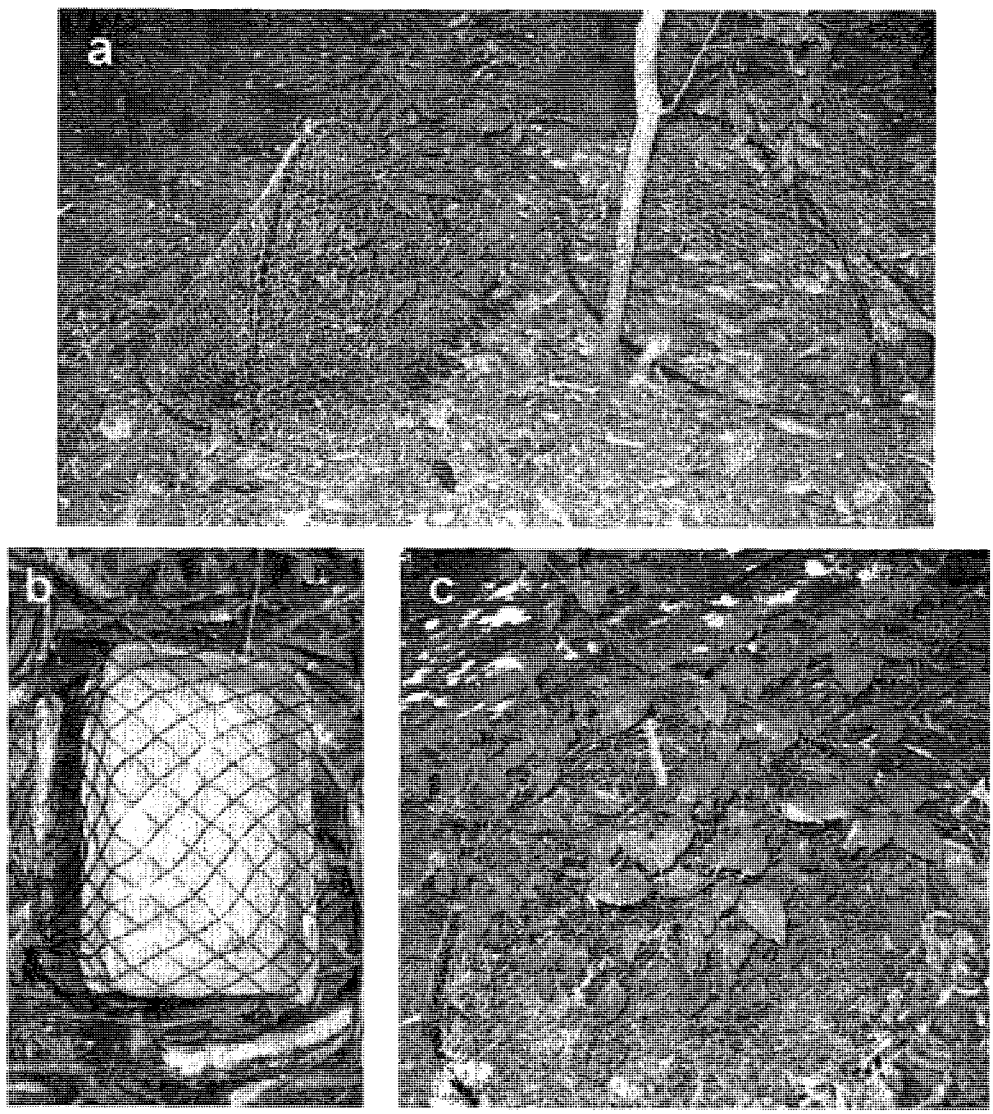


Figure 3.2

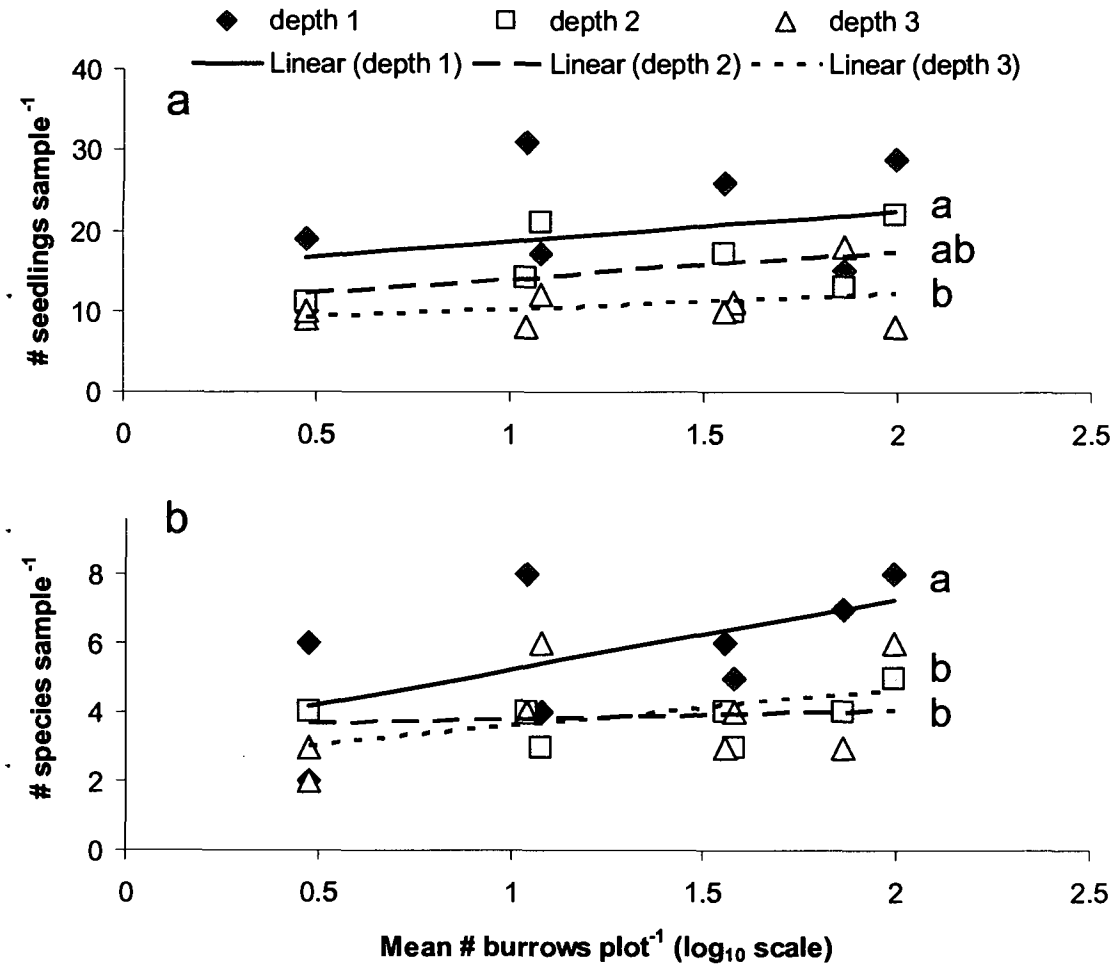

depth 1
depth 2
depth 3
Linear (depth 1)
Linear (depth 2)
Linear (depth 3)
a
seedlings sample-1
40
30
20
10
0
0
0.5
1
1.5
2
2.5
a
ab
b
b
species sample-1
8
6
4
2
0
a
b
b
Mean # burrows plot-1 (log10 scale)

Figure 3.3

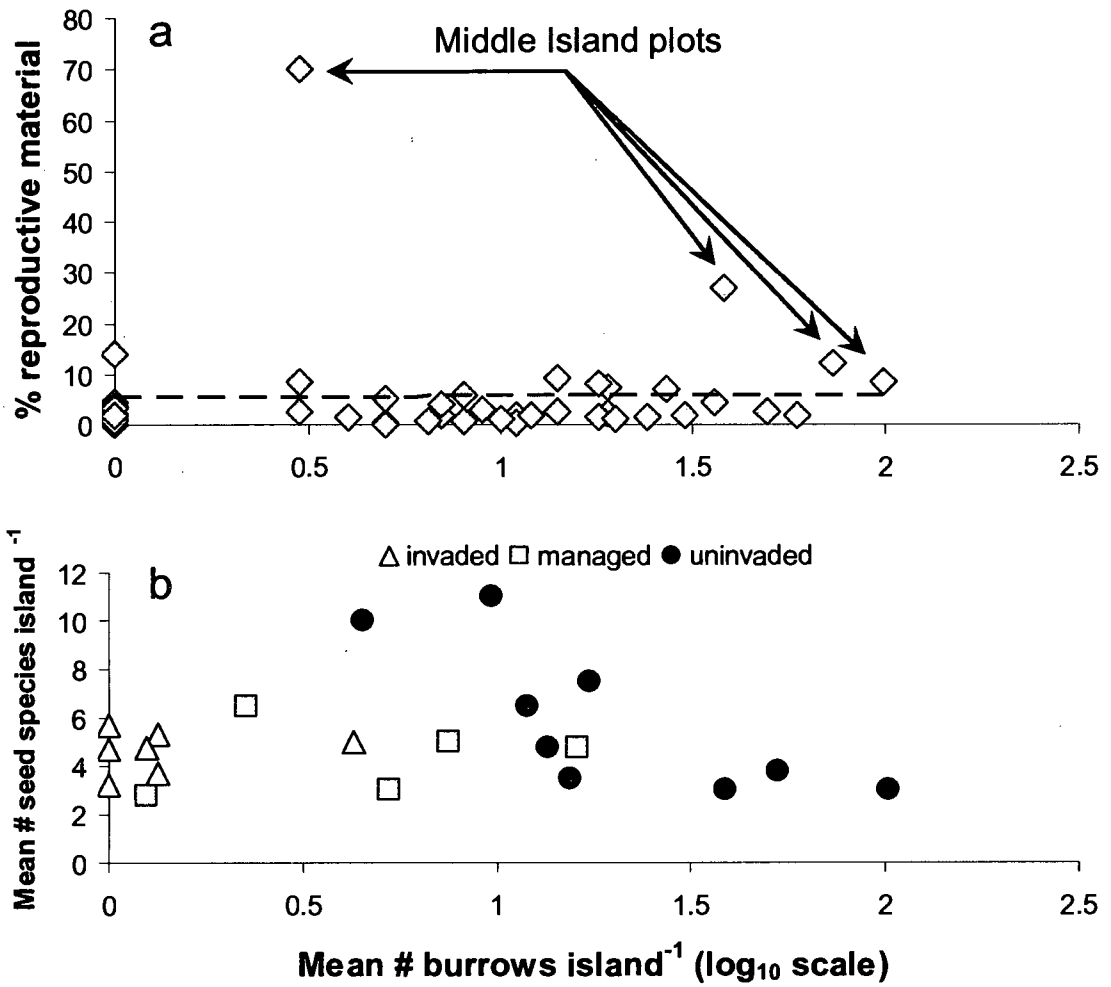

a
Middle Island plots
% reproductive material
80
70
60
50
40
30
20
10
0
0
0.5
1
1.5
2
2.5
b
△ invaded □ managed ● uninvaded
Mean # seed species island -1
12
10
8
6
4
2
0
0
0.5
1
1.5
2
2.5
Mean # burrows island-1 (log10 scale)

Figure 3.4

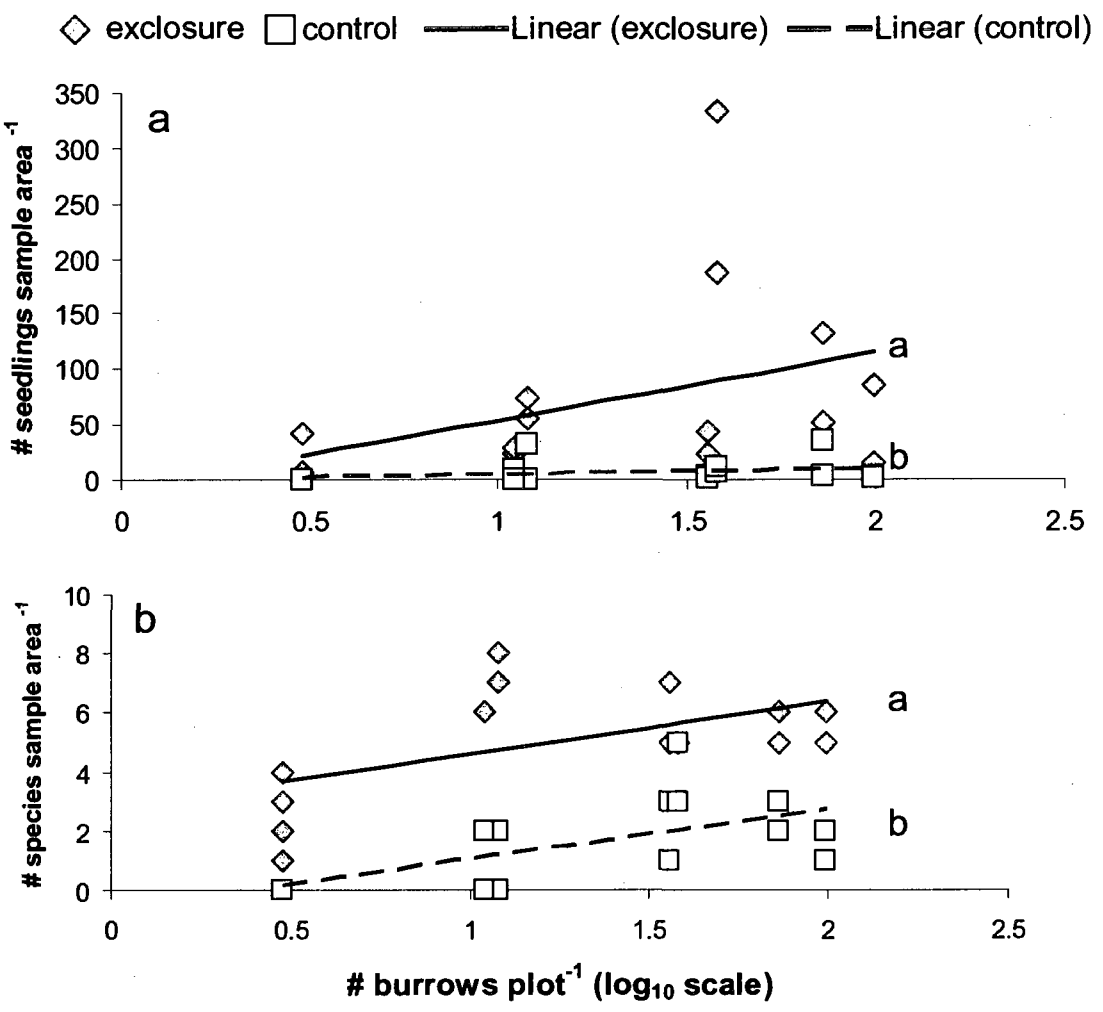

exclosure
control
Linear (exclosure)
Linear (control)
a
seedlings sample area -1
350
300
250
200
150
100
50
0
0
0.5
1
1.5
2
2.5
a
b
b
species sample area -1
10
8
6
4
2
0
0
0.5
1
1.5
2
2.5
a
b
burrows plot-1 (log10 scale)

Figure 3.5

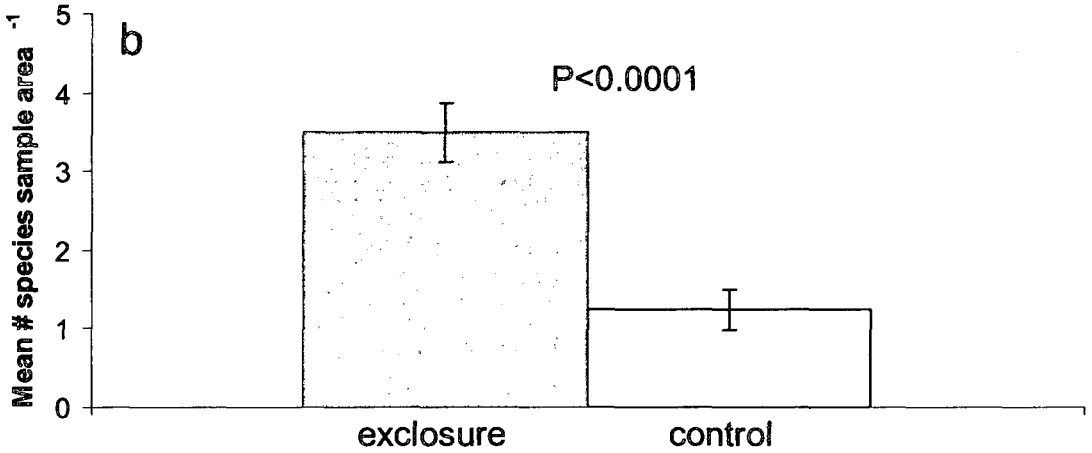
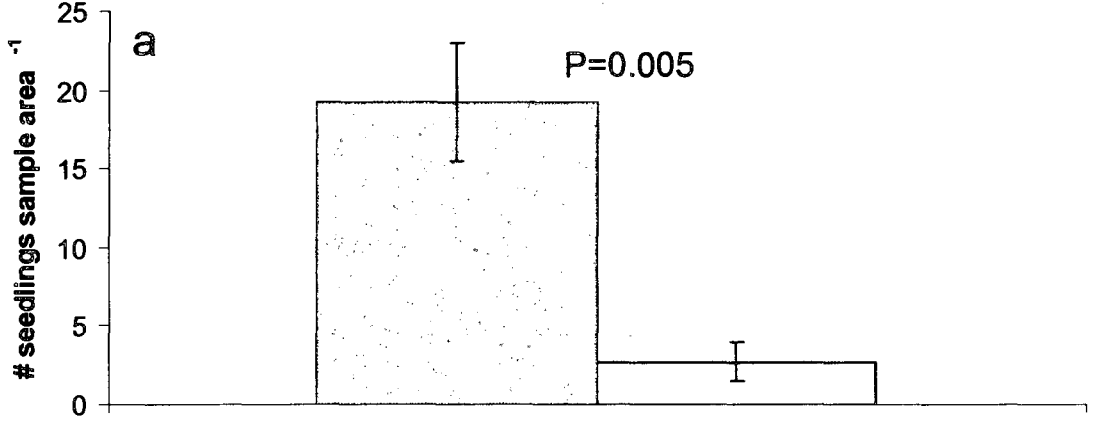

b
P<0.0001
Mean # species sample area -1
5
4
3
2
1
0
exclosure
control

Figure 3.6


a
P=0.005
# seedlings sample area -1
25
20
15
10
5
0

CHAPTER 4:

HERBIVORY IN INVASIVE RATS (*RATTUS EXULANS, R. RATTUS, R. NORVEGICUS*): CRITERIA FOR FOOD SELECTION[1]

[1] Grant-Hoffman, M.N. and P.S. Barboza (2009) Herbivory in invasive rats (*Rattus exulans, R. rattus, R. norvegicus*): Criteria for food selection. Prepared for submission in *Conservation Biology*.

ABSTRACT

Three species of rats (Pacific rat, *Rattus exulans*; Ship rat, *R. rattus*; and Norway rat, *R. norvegicus*) are widely invasive, having established populations in terrestrial habitats worldwide. These species are able to exploit a wide variety of foods and can devastate native flora and fauna. Rats can consume a variety of plant parts, but may have the most dramatic effects on plant populations through consumption and destruction of seeds. The vulnerability of vegetation to rat consumption is influenced by many factors including size of plant part to be consumed, and mechanical and chemical defenses. The relationship between the attributes of plants and their consumption by rats is not well documented. We reviewed the literature to find out what plant species and plant parts invasive rats are exploiting and common characteristics that may influence selection by rats. We also performed feeding trials in the laboratory with *R. norvegicus* to determine if seed hardness, size, and palatability influences rat consumptive choices. We found more reports of rat consumption of fruits and seeds versus other vegetative plant parts and more reports of consumption of smaller fruits and seeds. *R. norvegicus* are reported to consume proportionally more vegetative plant parts than either *R. exulans* or *R. rattus*, possibly due to their ground dwelling habits. In the laboratory we found that *R. norvegicus* preferred the smallest of three seeds presented. The seed coat of this seed was also the most preferred in taste tests. While large size and hard seed coats may deter rat feeding, these characteristics can be overcome if food is limited or the reward is large. Chemical defenses may be more effective in deterring rat consumption. By understanding

what characteristics rats are using to make food selections, scientists and managers can better manage vegetation in rat invaded areas.

INTRODUCTION

There are three species of widely invasive rats (Rodentia: Muridae): Pacific rats (*Rattus exulans*), ship rats (*R. rattus*), and Norway rats (*R. norvegicus*). These animals have successfully established populations in a wide range of habitats throughout the world, with devastating consequences for native flora and fauna (e.g., Atkinson 1985, Towns et al. 2006, Jones et al. 2008). Invasive rats reproduce rapidly and are able to adapt to almost every terrestrial habitat (Wilson and Ruff 1999). These rats can have especially large effects on island communities, where they often become the top predators (Courchamp et al. 2003, Towns et al. 2006).

R. exulans is the smallest of the three species (60 - 180 g body mass); these rats are capable climbers and can nest and feed in trees (King 2005). *R. exulans* originated in South-East Asia and spread throughout the Pacific with seafaring peoples as early as 1100BC (Atkinson 1985, King 2005). *R. rattus* is a larger species (120 - 225 g) that is also highly arboreal (King 2005). *R. rattus* spread from India across the Middle East and into Europe by 1000AD. Seafaring European explorers spread *R. rattus* through much of the world during the 1500s (Atkinson 1985, Yalden 1999). *R. norvegicus* is the largest of the three invasive rats (200 – 450 g). Although they are not good climbers, they are excellent swimmers and burrowers (Russell et al. 2005, King 2005). *R. norvegicus* likely originated in the steppes of central Asia and began spreading to Europe in the early to mid 1700s where they largely replaced *R. rattus* as the most common rat (Yalden 1999). Modern shipping accelerated the spread of *R. norvegicus* from Europe during 19th and 20th centuries (Atkinson 1985).

Rats are able to exploit a wide variety of foods because they have continuously growing incisors that allow them to break into the tissues of both plants and animals (Wilson and Ruff 1999, King 2005). Much attention has been paid to rats as adept animal predators (e.g., Towns and Daugherty 1994, Drever and Harestad 1998, Jones et al. 2008) and the cascading effects that this predation can have on vegetation (e.g., Fukami et al. 2006, Grant-Hoffman et al. 2009a). However less research has addressed the direct effects of rat herbivory on plant populations. The effects of invasive rats on animal populations are often much easier to discern than the subtle changes in plant populations, which may take generations to manifest. Rats directly consume vegetation (e.g., Allen et al. 1994, Campbell and Atkinson 2002), but one of the most dramatic ways that rats influence flora is through the consumption of seeds. Rodents may serve as seed dispersers that distribute seeds through caching (see review Price and Jenkins 1986), and as 'seed predators' that destroy seeds through consumption (McConkey and Drake 2002). The magnitude of the effect of seed predation by invasive rats on plant populations is poorly characterized or understood. By understanding how rats are making consumptive choices, scientists and managers can better manage plant populations affected by rat invasion.

The vulnerability of plants to herbivores is influenced by many factors. For example, relatively large food items or items with hard coats or other mechanical defenses (such as thorns or hairs) can preclude consumption by some herbivores, and for others it can increase handling time and the energy invested in processing the item before any energy or nutrients are returned from ingestion (Janzen 1971). In addition, mechanical defenses may increase the risk of injury to the consumer (Crawley 1983).

Plants are often laden with secondary compounds which can be lethal, cause sickness, or may interfere with digestion, thereby decreasing net energy intake (see review Rosenthal and Berenbaum 1991). Availability of a food source in time and space also influences preferences by the consumer. Food sources that are distributed in patches, providing a lot of food in a small area, are easier to find and exploit and generally preferred over items that are more sparsely dispersed (Janzen 1971, Crawley 1983, Pyke 1984). These factors, along with energy and nutrient content, influence how rats select plant species and plant parts to consume and thus how rats affect plant communities.

Through a literature review, we sought to identify the plant species and plant parts exploited by invasive rats and the food characteristics that influence consumption by rats. We also performed feeding trials in the laboratory with *R. norvegicus* to determine, in a controlled setting, if seed hardness, size, and palatability influenced rat consumptive choices.

METHODS

Literature review

Plant species

We identified articles for review through several electronic search engines including Web of Science (http://thomsonreuters.com/products_services/scientific/Web_of_Science), BioOne (http://www.bioone.org), BIOSIS previews (http://www.thomsonreuters.com/products_services/scientific/BIOSIS_Previews), and Google Scholar (http://scholar.google.com/) using key words such as "*Rattus*", "seeds", and "vegetation". We included only articles that reported substantial evidence of rat consumption of plants through visual observation of consumption, laboratory or field feeding trials, physical evidence (chewed seeds or plants), stomach contents, plant remains in husking stations, or plant material collected from feces. We only included accounts of *R. exulans*, *R. rattus*, and *R. norvegicus*, since these are the most widespread rodent invaders. We compiled a list of all seeds and plant parts consumed by these species (Appendix 4.1) and some general characteristics of the reproductive parts (e.g. fruit, capsule, cone) and seeds.

Analysis

We performed G-tests for goodness of fit on numbers of reports of consumption of seeds and fruits versus vegetative plant parts (Sokal and Rohlf 1994). We used an expected ratio of 1 to 1. This is a conservative comparison since vegetative plant parts

must be present before reproductive plant parts can be produced and therefore are usually available for a longer period of time. We excluded references that were biased towards seed consumption (where only seeds or fruits had been used in feeding trials or where results were from husking stations).

We used the median values reported for the size of reproductive parts and seeds. Foods were assigned to 9 size classes ranging from 0-5 mm to >200 mm (in 5 mm categories up to 30 mm, then 30-99 mm, 100-199 mm, and >200 mm) to count the frequency of reported consumption. We repeated this analysis for reports of New Zealand reproductive parts of shrubs and trees consumed by rats, and for reproductive parts of common New Zealand shrubs and trees (from Poole and Adams 1994). We used a Chi-square goodness of fit test to determine if the distribution of reproductive part sizes of native New Zealand shrubs and trees described in the literature as consumed by rats was statistically different from the 'null model' distribution of reproductive parts of common New Zealand trees and shrubs (Sokal and Rohlf 1994). To increase the numbers of observations we reduced our number of size classes to five (0-5 mm, 5-10 mm, 10-20 mm, 20-30 mm, and >30 mm). In addition, we compared the percentages of seeds and reproductive parts versus vegetative parts consumed by each of the three rat species. We recognize that this method does not consider preferences. However, we did not find enough studies that considered food preferences to rank a significant portion of the plants consumed. Our analyses did not consider the amount of food consumed, the availability of other foods, origin of plant species (native or non-native), or impacts on plant populations because the published data were not sufficient for those comparisons.

Plant families

We examined which families of New Zealand plants are more or less vulnerable to rat consumption. We limited our analysis to native trees and shrubs of New Zealand because data for the consumption of this flora by rats were most complete. For this analysis, we used Poole and Adams (1994) as our primary reference for plants in New Zealand since this reference is likely to include the most common species and consumption of rare species may be hard to detect. Since seeds and fruits are reported as being consumed more often than vegetative parts, we considered only consumption of seeds or fruits. We assigned families to one of three categories of rat tolerance: vulnerable, resistant, or intermediate. Vulnerable plant families were those in which seeds or fruits of at least half of the genera in New Zealand were listed as consumed by rats. Resistant plant families did not contain any genera where seeds or fruits were listed as consumed by rats. Intermediate plant families were those with seeds and fruits of only one genus were consumed by rats. We excluded plant families where only one genus was found in New Zealand. We also excluded genera listed as rare or only locally distributed since the ability to detect rat consumption would be more difficult for these genera. This analysis yielded 6 vulnerable families, 14 resistant families, and 5 intermediate families. We compiled some general characteristics of these families. We also performed G-tests for goodness of fit on numbers of reports of chemical defenses in vulnerable versus resistant plant families (Sokal and Rohlf 1994). We used an expected ratio of 1 to 1, indicating equal abundance of both vulnerable and resistant plant families.

Laboratory feeding trials

Subjects

We held 15 male brown *R. norvegicus* in a laboratory setting for 60 days under Assurance #06-02 from the University of Alaska Fairbanks Institutional Animal Care and Use Committee and Permit # 08-057 from the Alaska Deptartment of Fish and Game. The laboratory room was maintained at 21°C and 30% humidity in a daily cycle of 12 h light and 12 h dark by using fluorescent and infrared lights during the day and night respectively. Rats were allowed to acclimate to the cages and ambient conditions for 10 days. We used adult animals that were retired breeders (> 8 months of age) of the BN/RijHsd line (Harlan Inc., Indianapolis, IN). Animals were held in individual cages (dimensions 26.67 cm x 48.26 cm x 20.32 cm) with a litter of wood shavings. Water was available *ad libitum* from drinker bottles throughout the study. Study animals maintained body mass (352 ± 13 g) throughout the study on a diet of rat chow (Mazuri Rodent Pellets, PMI Nutrition International, Richmond, IN). We measured food intakes of rat chow in 2 periods of 12 h each day at the start of the study (day 0-3). We found that rats consumed more food at night than during the day; dry matter intakes were 5.6 ± 1.9 g during the day and 11.1 ± 1.6 g at night. Consequently, we studied food selection only during nocturnal periods.

Characteristics of intact seeds

We were unable to test seeds collected in the field (New Zealand) due to difficulties bringing these seeds and fruits into the United States. Therefore, we chose

seeds that were readily available from local grocery stores to serve as proxies for seeds found in the field. We used three seeds (intact with seed coats) to examine the preferences of *R. norvegicus*: black oil sunflower seeds (*Helianthus annuus*), walnuts (*Juglans regia*), and roasted peanuts (*Arachis hypogaea*). These seeds are within the size range of seeds and fruits produced by plant species that we found sensitive to invasive rats on islands (Table 4.1, Grant-Hoffman et al. 2009a). For example, walnuts are similar in size to *Pittosporum crassifolium*, sunflower seeds are similar in size to *Pseudopanax lesonii*, and peanuts are similar in size to *Coprosma macrocarpa* (Tables 4.1, 4.2). Seeds of *P. crassifolium* and *C. macrocarpa* were consumed by *R. norvegicus* in field feeding trials, while seeds of *P. lessonii* were not (Grant-Hoffman et al. 2009b). The laboratory trials focused on testing the effects of seed coats on rat consumption because the physical and chemical character of the seed coat may be the most important deterrent to seed predation.

We tested the hardness of the shells of 20 individual seeds for each of the three seed species (sunflower, walnut, and peanut). We used a Humboldt pressure gauge to test the amount of pressure needed to crack the seed coat (Humboldt MFG CO, Chicago, IL, Model H-4133). We used a bit that closely approximated the area of rat teeth (3.5 mm) based on measurements from specimens of *R. norvegicus* from the University of Alaska Fairbanks Museum (UAF Loan #2007.023.Mamm). Breaking strain of the seed coats was compared using ANOVA (SAS Institute 2002).

Taste test for seed coats

Taste tests were performed with a standard matrix of unflavored gelatine (Knox original gelatine unflavored, Kraft foods North America, Tarrytown, NY). Each animal was given approximately 15 ml of gelatine. We familiarized the rats with this test matrix for 4 days and encouraged consumption by initially mixing 5 ml of peanut butter (Private Selection Creamy Peanut Butter, Inter-American Products, Cincinnati, OH) with approximately 236 ml of gelatine (7.33 g dry gelatine per 236 ml of water; day 5-16). Gelatine was offered in a metal dish (15 x 8 x 5 cm) for 12 hours (8:00 pm to 8:00 am). During this adjustment period both rat chow and water were available *ad libitum.*

Taste tests were performed on only the shells of sunflower seeds, walnuts, and peanuts. Each shell was crushed and mixed into the same unflavored gelatine matrix (day 17) in a ratio of 5 ml of crushed shell to 236 ml (1 cup) of liquid gelatine. Rat chow was withheld during the 12 hour (8:00 pm to 8:00 am) trial period. We simultaneously offered rats 6 ± 1 g (about 15 ml) of each gelatine-shell mixture, totaling approximately 18 g of food offered (whole mass of gelatine mixture). Thus, rats would have had to consume more than one food choice to meet their average food intake of 11 g of dry rat chow. We observed rats for 10 minutes every 45 minutes for 5 hours to monitor the order in which they selected each food.

In addition to totaling the number of rats that consumed each item we performed G-tests for pairwise comparisons (sunflowers vs. walnuts; sunflowers vs. peanuts; and peanuts vs. walnuts). For each test we considered whether an item was preferred or not. If

a rat did not make a clear choice between the two items being considered we excluded it from this analysis.

Seed consumption trials

Seeds (black oil sunflower seeds, peanuts, and walnuts) and rat chow were provided *ad libitum* for 7 days to familiarize the rats with the test foods (day 36-43). During this time we provided rats with seeds that were both open and intact to facilitate learning a new food source. At the beginning of these trials animal weights were similar to those at the start of the study (mean weight day 1 = 351 g, mean weight before trial, day 34 = 353 g).

Rat chow was withheld for 12 h during each measurement of seed intake. Each animal was provided with approximately 18 g of seeds (about 6 g of each food item) for the night. These weights were based on the mean amount of dry edible material (shell not included) found in each food item. Thus, rats had to choose at least two items to match the same daily intake of rat chow. Measures of seed intake were repeated for a total of three nights alternating with three 'rest' nights during which rats were offered their regular diet of rat chow *ad libitum* (day 44-48). Food was weighed at the beginning and end of each 12 hour trial. We used ANOVA to compare amounts eaten of each seed (SAS Institute v.9.1 2002, Cary, NC). The response variable was the mean amount (dry weight, g) of each seed species consumed by all rats during each trial.

RESULTS

Literature review

Characteristics of plants consumed by rats

We found significantly more reports of rats consuming seeds than other parts of plants for both *Rattus exulans* ($\chi^2_{(1)}$ =18.42, P<0.001) and *R. rattus* ($\chi^2_{(1)}$ =28.42, P<0.001, Table 4.3). However, there were proportionally more accounts of vegetative plant parts being eaten by *R. norvegicus* (42% of total reports) than either by *R. exulans* (21%) or *R. rattus* (13%), and there was not a significant difference between reports of consumption of vegetative plant parts versus seeds or fruits for this species ($\chi^2_{(1)}$ =0.57, P=0.45). We found that plant species with reproductive parts and seeds less than 15 mm were most frequently consumed (Fig. 4.1). Reproductive parts between 5 and 10mm were most preferred by all three *Rattus* species. However, this may reflect seeds available. A survey of sizes of reproductive parts of shrub and tree species in New Zealand showed that smaller seeds may be more abundant in general (Fig. 4.2). Reports of consumption of reproductive parts of New Zealand shrub and tree species were statistically different from the general size distribution of reproductive parts of New Zealand shrub and tree species for *R. exulans* only ($\chi^2_{(4)}$ =30.13, P<0.001). This species was reported to consume fewer than expected larger (over 20 mm) reproductive parts and more than expected small reproductive parts (less than 5 mm) (Figure 4.2a, b). Reports of consumption of reproductive parts of New Zealand shrub and tree species were not statistically different from the general distribution for either *R. rattus* ($\chi^2_{(4)}$ =5.66, P=0.23) or *R. norvegicus* ($\chi^2_{(4)}$ =7.71, P=0.10; Fig. 4.2a, b).

Six of 25 plant families in New Zealand were classified as vulnerable to rat consumption because more than 50% of the genera were reported to be consumed by rats (Table 4.4). We found that the type of reproductive part was variable for both vulnerable and resistant families. We found more reports of chemical defenses within resistant families (50% of families reported had reports of chemical defenses) than in vulnerable families (30% of families reported had reports of chemical defenses); however this difference was only marginally significant ($\chi^2_{(1)}$ =3.30, P=0.07). A wide variety of chemical defenses were located in different plant parts including seeds and leaves.

Laboratory feeding trials

Fourteen of 15 subjects consumed gelatine with peanut butter. Ten of 15 animals consumed at least one gelatine cube with the crushed shell of the three food choices. Nine of these 10 animals consumed the sunflower seed mixture, 4 of 10 animals consumed the peanut mixture, and 5 of 10 animals consumed the walnut mixture. G-tests indicated that sunflowers were significantly preferred over both walnuts (χ^2 = 10.0, p=0.002; 5 animals clearly chose between these two choices) and peanuts (χ^2 = 9.0, p=0.003; 8 animals clearly chose between these two choices). The shells or peanuts and walnuts were equally preferred: of four animals that clearly chose between peanuts and walnuts, two preferred peanuts and two preferred walnuts.

We found walnut shells required on average 0.91 kg mm^{-1} of pressure to break the seed coat, peanuts required 0.09 kg mm^{-1} of pressure, and sunflower seeds required 0.36 kg mm^{-1} of pressure. All differences in seed hardness were significant ($p<0.0001$, Table 4.2). Rats consumed significantly ($p<0.0001$) more sunflower seeds (5.2 ± 0.34 g dry matter) than peanuts (2.4 ± 0.13g dry matter), but did not consume walnuts.

DISCUSSION

We found more reports of rats eating seeds than vegetative plant parts. Seed predation by rats likely reflects the higher concentrations of energy and nutrients of seeds versus leaves and other plant parts (Janzen 1971). The high nutrient content of seeds partly compensates for the greater cost of time and energy to handle defensive seed coats and skins when compared with vegetative plant parts. In addition, fruits and seeds are often distributed in clusters (Janzen 1971, Crawley 2000), which may make them easier to find and exploit and thus increases their attractiveness as a food source (Pyke 1984).

Although rats may serve as seed dispersers in areas where they are native (Price and Jenkins 1986) and in areas where they are invasive (Williams et al. 2001, Grant-Hoffman et al. 2009b), rats often destroy seeds in the process of consuming the fruit (McConkey and Drake 2002). Plant species that do not reproduce vegetatively are most vulnerable to seed predation by rats because destruction of the seed is destruction of a potential plant and these plants reproduce only with seeds (Crawley 2000). Adult plants can often recover from vegetative herbivory (Janzen 1971, Crawley 2000), but if reproduction and recruitment of seedlings into the adult community is significantly reduced, plant populations may suffer. This may be especially true for slower-growing woody plants which may have lower seed output than quicker growing herbaceous species.

We found a higher percentage of reports of *R. norvegicus* eating vegetative plant parts than either *R. exulans* or *R. rattus*. This is likely partly because *R. norvegicus* is generally more ground dwelling and is a poor climber (King 2005). Thus, the only seeds

readily available to this species are seeds that have fallen to the ground, or are growing close to the ground. These seeds may be less aggregated in space and time and thus a less attractive food source (Crawley 2000). *R. norvegicus* may therefore supplement their diets with vegetative plant parts that are more readily available to ground dwelling animals. Birds, lizards, and other native dispersers may still have a competitive advantage over *R. norvegicus* because they can consume seeds directly from the branches of trees (Crawley 2000). In contrast, both *R. exulans* and *R. rattus* are adept climbers and can directly compete with other dispersers by taking seeds and fruits directly from branches (King 2005). Climbing also increases the number and variety of seeds and fruits available to *R. exulans* and *R. rattus*.

The size of seeds and fruits may play an important role in which seeds and fruits are preferred. In our feeding trials, we found that the *R. norvegicus* preferred the smallest seeds presented (sunflower seeds). In addition, our literature review found more reports of smaller-fruited (0-10 mm) and seeded species being consumed by all three rat species, although this may simply reflect seed availability and was only significant for *R. exulans*. All three rat species may cache their food (Vander Wall 1990), and smaller items can be more easily moved for storage. Some small seeds can pass through rat digestion unharmed; for example, seeds of *Macropiper excelsum* (seed size 1.5-2.5 mm) are dispersed by *R. rattus* (Williams et al. 2001). One study found seeds that successfully passed through the digestive tract of *R. rattus* were smaller than average seeds collected from fruits (Bourgeois et al. 2005). The trend of smaller fruits and seeds being preferred was most pronounced for *R. exulans*, the smallest of the tree species; and it may be more

limited by body size than the other two species. While smaller seeds may be preferred, larger seeds, when consumed, may be more likely to be destroyed by rats and may represent greater impacts on the plant species. Larger seeds often represent slower growing plants that are investing proportionally more resources in a single seed (Bazzaz et al. 2000, Leishman et al. 2000).

Another characteristic which can affect handling time and preference is hardness of seed coat. Hardness of the seed coat may have been a deterrent to consumption of walnuts but not sunflower seeds. In our laboratory experiments we found that although rats would eat walnuts (the hardest choice presented) when the shell had been opened, they would not open the shell to consume the contents even though the energy density of the walnut was greater than the other two choices (Table 4.2). Other studies have also found that *R. norvegicus* have aversions to hard food in the laboratory (Sako et al. 2002). However, if choices are limited or the reward is very large, the increased handling time and potential for injury may be worth the risk as shown by *R. rattus* consuming *Cocos nucifera* (coconut), a very large and very hard seed (Marshall 1955, Fall et al. 1971). In addition in our laboratory trials, *R. norvegicus* consumed intact sunflower seeds more than intact peanuts even though the coats of sunflower seeds were much harder than those of the peanuts (Table 4.2).

Taste may influence the handling of seed coats. Animals use texture, smell, and taste to guide their selection of seeds and fruits to favor high nutrient contents or low handling costs (Drewnowski 1998). We found that the preferred seed in our trials (sunflowers seeds) was also the one with the preferred seed coat. Since our rats were

unfamiliar with to these food sources, preference for the seed coat of sunflower seeds was not learned and must be based on sensory cues like taste. In addition to indicating nutrition, taste can also indicate danger in the form of a chemical defense of the plant. Seed coats often contain astringent compounds such as tannins and other toxic phenols that deter consumption (McGee 2004). Many secondary chemicals have a distinct smell or taste that can warn and deter herbivores (Rosenthal and Berenbaum 1991) and chemical defense may play an important role in deterring rat consumption (Gonzalez-Coloma et al. 1990). *R. norvegicus* can learn food preferences based on palatability (Barbano and Cador 2005) and nutrient content (Scalfani and Nissenbaum 1988). In addition, herbivores can quickly determine levels of plant secondary metabolites in plants based on small amounts of food taken in, and modify their foraging behavior and feeding to keep physiological levels of these chemicals below toxic levels (Freeland and Janzen 1974, Sorenson et al. 2005). This gives these animals a powerful way to make food selections.

It is unlkely that herbivores can completely avoid plant secondary compounds; thus they must regulate their intake (Iason and Villalba 2006). Plant secondary metabolites vary in their level of toxicity, although most if not all are dose-dependant (Iason and Villalba 2006). Herbivores must balance the metabolic costs of detoxifying and excreting plant secondary metabolites with nutrient intake (Iason and Villalba 2006). Rats and other rodents may also acquire a tolerance or resistance to plant chemical defenses by changing their feeding patterns and physiology. For example, salivary proteins are induced by tannin consumption in rats (Mehanso et al. 1987). Similarly,

absorptive and metabolic pathways may also be altered in rodents after repeated exposure to some toxins (Harborne 1993, Sorensen et al. 2004, Sorensen et al. 2005,). Herbivores may also regulate intake of plant secondary metabolites behaviorally. For example, mice are able to choose combinations of foods containing tannins and saponins that reduce their toxic properties because these chemicals combine in the intestinal tract (Freeland et al. 1985).

Chemical defenses may be more prevalent in certain plant families (Rosenthal and Berenbaum 1991), and we found that vulnerable plant families had fewer accounts of chemical defenses than resistant plant families (Table 4.4). However, this difference was not statistically significant. The majority of our reports were on islands, and plant secondary metabolites may be low on islands because historically these plants have experienced lower herbivory rates by mammals than mainland plants (Courchamp et al. 2003).

FUTURE RESEARCH

There is growing literature on the effects of rat sensitivity to plant secondary compounds (e.g., Spurr et al. 2001). However, much can still be learned. For example, it has been estimated that less than 1% of terpenoids have been studied as herbivore deterrents (Watkins et al. 1996). Mechanical defenses and size of seeds and reproductive parts do not entirely explain food preferences of rats, and chemical defenses may be functioning. Knowledge of sensitivity to secondary chemicals in invasive rats can be an important tool for managers. Laboratory trials with these three rat species could determine their sensitivity to secondary chemicals. With this information scientists and managers could identify seeds that may be well protected from rat predation. This type of research could have far reaching conservation applications. Plant secondary metabolites can influence the way animals are foraging and thus influence rat survival, growth, and reproduction (Barboza et al. 2009). This information could also be used to deter rat population growth or spread into unwanted areas. For example, by stocking certain areas with plants that are unpalatable to rats, managers could deter their movement into highly valued conservation areas. In addition, solutions with plant secondary metabolites can be used as a non-toxic herbivore deterrent (Crocker et al. 1993, Watkins et al. 1996). These deterrents could help to protect plants until they are of a size and age to withstand rat consumption.

We only briefly considered consumptive preferences of rats when they are presented with several food choices. Apart from our laboratory trials we found one other study considering herbivorous preferences with one of these three rat species (Cheng et

al. 2005). This study considered *R. norvegicus* along with two native rodent species and did not find clear preferences of plants for *R. norvegicus*. Focused studies on preference can allow scientists to rank characteristics which are important in deterring rat consumption. This would allow a more comprehensive ranking of sensitive plant species and may provide a tool for monitoring the effects of herbivores on plants (Bryant and Reichardt 1992; Bryant et al. 1994).

In areas where animal prey available to rats are abundant, easy to catch, and easy to consume, pressures of rats on vegetation may be negligible. However, often animal prey can be quickly exhausted or can be seasonally or spatially variable (e.g., Drever and Harestad 1998, review Jones et al. 2008), making vegetation a significant contributor to rat diets. Thus, the vulnerability of plant species will also depend on the availability of animal food sources. We did not find studies that directly link fluctuations in rat diet to consequences for sensitive plant populations even though there have been studies on the variability of rat diets (e.g., Daniel 1973, Gales 1982, Sugihara 1997), and the effects of rat populations on plant production in general (Ruscoe et al. 2005, Harper 2005). The relationships between invasive rats and sensitive species of plants can be difficult to discern because there can be a significant time lag in plant population responses, especially with longer lived plant species. However, by incorporating information about seed and seedling community population fluctuations with rat diet and population fluctuations, scientists and managers can begin to understand this complex pathway. By understanding this pathway, restoration efforts after rat eradication, and management efforts in the presence of invasive rats can be comprehensive. For example, planting

sensitive plant species at a time when animal food sources are abundant may provide some protection for these species and allow them to reach a less vulnerable stage.

CONCLUSIONS

Overall, we found more reports that rats consume seeds and fruits versus other plant structures. However, *R. norvegicus* may pose a lesser threat to seed communities than either *R. exulans* or *R. rattus*, likely due to their ground dwelling habits. In addition, we found that although hard seed coats and large reproductive parts or seeds may be deterrents to rat consumption, these characteristics do not provide absolute protection. Rats are versatile eaters, and given a limited selection or a large reward rats can overcome seed hardness and size. Chemical defenses may be more effective. By understanding how rats choose what to eat we can identify vulnerable seeds and thus potentially vulnerable plant species. With this knowledge managers can better prioritize which plants to protect if rats cannot be removed, or concentrate on which plants to restore and how to accomplish this if rats can be removed.

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Table 4.1 – Plant species found to be vulnerable to rat invasion on islands in New Zealand (Grant-Hoffman et al. 2009a) along with general characteristics of reproductive parts and seeds. Vulnerability is based on significantly lower seedling numbers in a sampling area may not always result from consumption of seeds (Grant-Hoffman et al. 2009b). References in bold indicate vegetative parts only reported as eaten.

Family	Plant species	Rat species	Plant part eaten	Reproductive part	Reproductive part characteristics	Reproductive part size	Seed size	Reference
Araliaceae	*Pseudopanax lessonii*	*R. exulans*	**leaves, petiole, shoot apex**	**berry**	**coriaceous**	**6-7mm**	**5-7 mm**	Campbell 1978
Moraceae	**Streblus banksii*	*R. exulans*	fruit, bark	drupe	fleshy	5-6mm	5-6 mm	Campbell 1978
Piperaceae	*Macropiper excelsum*	*R. exulans*	fruit, leaf petoiles, twigs	drupe many close set	fleshy	2-3mm drupe closeset	1.5-2.5 mm	Campbell 1978, Williams et al. 2000
Pittosporaceae	*Pittosporum crassifolium*	*R. exulans*	fruit	subglobose capsule	fleshy	20-30mm	3-6 mm	Campbell 1978
Rubiaceae	*Coprosma macrocarpa*	*R. exulans*	fruit, bark, twigs, seedlings	drupe	fleshy	10-25mm	3-5 mm	Campbell 1978

Table 4.1 continued

Piperaceae	*Macropiper excelsum*	*R. rattus*	fruit (seeds intact)	drupe many close set	fleshy	2-3mm drupe closeset	1.5-2.5 mm	Campbell 1978, Williams et al. 2000
Piperaceae	*Macropiper excelsum*	*R. norvegicus*	fruit	drupe many close set	fleshy	2-3mm drupe closeset	1.5-2.5 mm	Campbell 1978
Pittosporaceae	*Pittosporum crassifolium*	*R. norvegicus*	fruit	subglobose capsule	fleshy	20-30mm	3-6 mm	Grant-Hoffman et al. 2009b
Rubiaceae	*Coprosma macrocarpa*	*R. norvegicus*	fruit	drupe	fleshy	10-25mm	3-5 mm	Grant-Hoffman et al. 2009b

*formerly *Paratrophis banksii*

Table 4.2 – Characteristics of food items used during feeding trials based on edible portions. Sunflower = black oil sunflower seeds (*Helianthus annuus*), Peanut = roasted peanuts (*Arachis hypogaea*), Walnut = walnuts (*Juglans regia*). [1]Nutritional information is referenced from USDA 2007 and Mazuri Rodent Pellents 2008.

Food	Whole mass (g seed^{-1})	Moisture content (g whole mass^{-1})	[1]Energy (KJ g^{-1})	[1]Protein (g^{-1})	[1]Lipid (g^{-1})	[1]Carbohydrate (g^{-1})	Hardness (lbs of pressure)	Size (mm)
Sunflower	0.036	0.001	24.45	0.2078	0.5146	0.2	8	3 x 7
Peanut	1.547	0.002	24.48	0.2368	0.4966	0.2151	2	8 x 31
Walnut	5.869	0.054	27.38	0.1523	0.6521	0.1371	20	30 x 34
Rat Chow	7.029	0.349	12.55	0.24	0.065	0.494	—	13 x 24

Table 4.3 – Summary of results from Appendix 4.1.

	Plant part eaten (# of reports)		Reproductive part size (mm)		Seed size (mm)	
Rat species	fruit or seed	vegetative	mean	range	mean	range
Rattus exulans	46	11	24.8	1-300	9.5	0.8-30
R. rattus	49	6	21.8	2-300	13.5	0.7-300
R. norvegicus	20	12	29.8	2-250	16.3	1.5-130

Table 4.4 – Vulnerable and resistant woody plant families in New Zealand with general notes on types of fruits and chemical defenses. Number of genera consumed refers to reports of seeds or fruits being consumed. '*' indicates only vegetative part reported as eaten.

Vulnerable						
	# genera consumed	**total # genera**	**Type of fruit**	**chemical defense**	**Notes**	**Relevant references**
Araliaceae	5	5	berry or drupe	—	—	—
Eleocarpaceae	2	2	capsule or drupe oily endosperm	—	used for food	Woodland 1997
Oleaceae	2	2	berry, capsule, drupe, samara	—	used for food	Woodland 1997
Podocarpaceae (Conifer)	4	8	fleshy aril and ovule	—	may mast as a defense	Norton and Kelly 1988
Rosaceae	4	4	diverse fruit	amygdalin (seeds of genus *Prunus*), cyanogenesis common	used for food	Woodland 1997, Rosenthal and Berenbaum 1991
Solonaceae	2	2	berry or capsule	anthocyanins, alkaloids common	used for food	Woodland 1997, Rosenthal and Berenbaum 1991, Watkins et al. 1996
Resistant						
Convolvulaceae	0	2	capsule	—	used for food	Woodland 1997
Cunoniaceae	0	2	capsule or nut, copious oily endosperm	—	—	—
Epacridaceae	0	7	capsule or drupe	—	—	—
Ericaceae	0	2	berry, capsule, drupe	phenolic acids occur	used for food	Woodland 1997, Cipollini and Stiles 1992

Table 4.4
continued

Escalloniaceae (Grossulariaceae)	0	3	capsule or berry	cyanogenesis occurs	---	Bjarnholt et al. 2008
Fabaceae	0	6	dry or fleshy legume	cyanogenesis common	used for food	Woodland 1997, Rosenthal and Berenbaum 1991
Loranthaceae	0	4	berry or drupe	---	---	---
Monimiaceae	*1	2	drupes or nuts enclosed in perianth	---	---	---
Myrtaceae	*1	6	berry, drupe, capsule, nut	monoterpene	used for food	Woodland 1997, Lerdau et al. 1994
Ranunculaceae	0	2	berry or dry fruit	cardenolides occur	some poisonous	Woodland 1997, Rosenthan and Berenbaum 1991
Rhamnaceae	0	2	drupe or nut	---	---	---
Rutaceae	0	2	berry or drupe, hesperidium or schizocarp	Limonoids, furanocoumarin occur	used as food	Woodland 1997, Rosenthal and Berenbaum 1991
Santalaceae	0	2	drupe or nut	---	used for food	Woodland 1997
Sapindaceae	0	2	berry, capsule, drupe, nut	caffeine, cyanolipid occur	used for food	Woodland 1997, Rosenthan and Berenbaum 1991
Intermediate						
Asteraceae	1	5	achene, often with pappus	—	used for food	Woodland 1997
Lauraceae	1	3	berry or drupe	cinnamon	used for food	Woodland 1997
Mavaceae	1	2	capsule, schizocarrp, rarely berry	---	used for food	Woodland 1997
Proteaceae	1	2	achene, drupe, follicle, nut	---	pollinated by mice	Woodland 1997
Verbeneaceae	1	2	drupe, rarely capsule	---	---	Woodland 1997

FIGURE LEGENDS

Figure 4.1 – Histograms of sizes of reproductive parts and seeds consumed by three species of invasive rats (*R. exulans*, *R. rattus,* and *R. norvegicus*).

Figure 4.2 – Histograms of sizes of reproductive parts of (a) New Zealand shrub and tree species reported as consumed by three species of invasive rats (*R. exulans*, *R. rattus,* and *R. norvegicus*) and (b) common New Zealand shrub and tree species from Poole and Adams (1994).

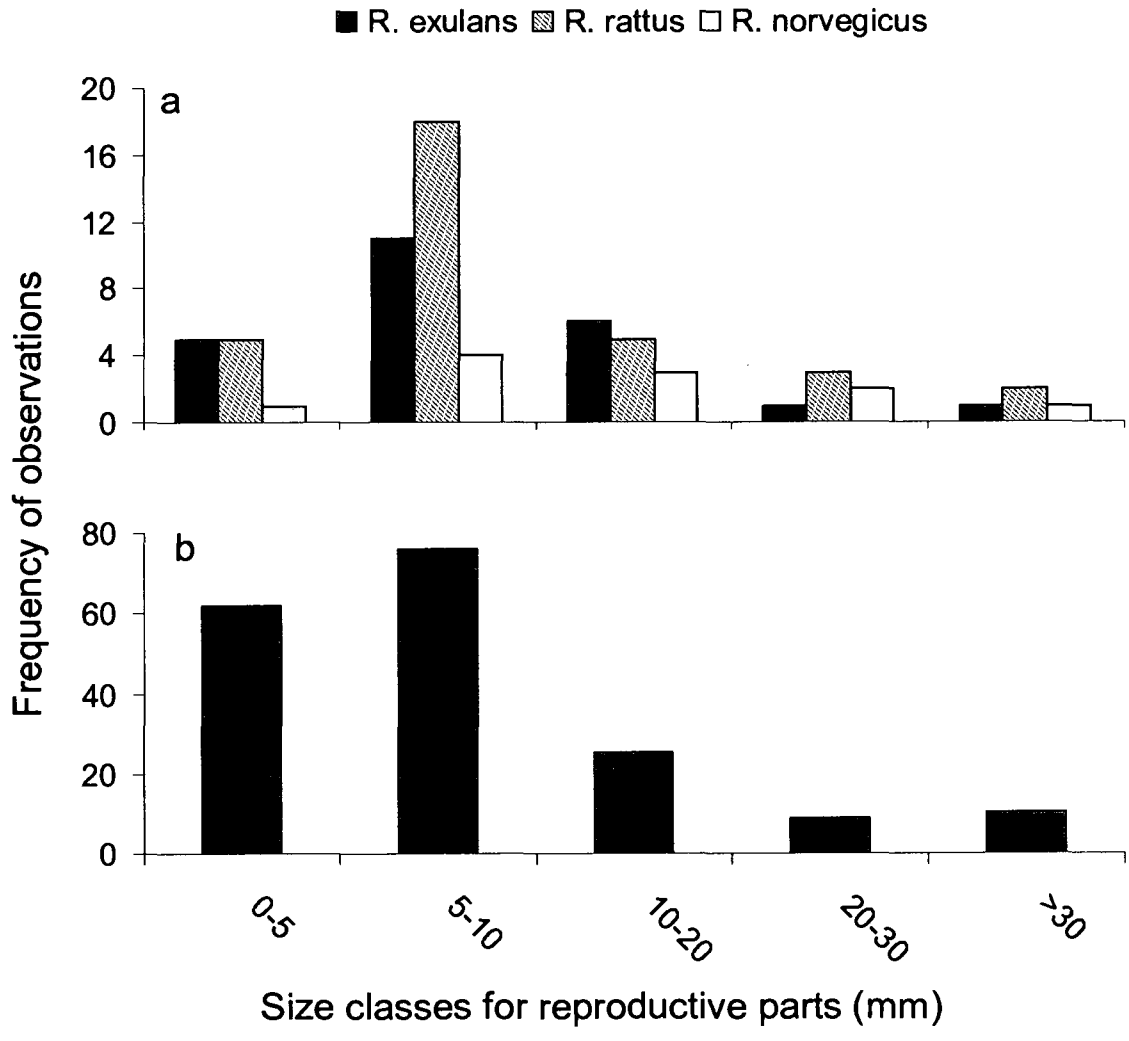
R. exulans
R. rattus
R. norvegicus
a
b
20
16
12
8
4
0
80
60
40
20
0
Frequency of observations
0-5
5-10
10-20
20-30
>30
Size classes for reproductive parts (mm)

Figure 4.1

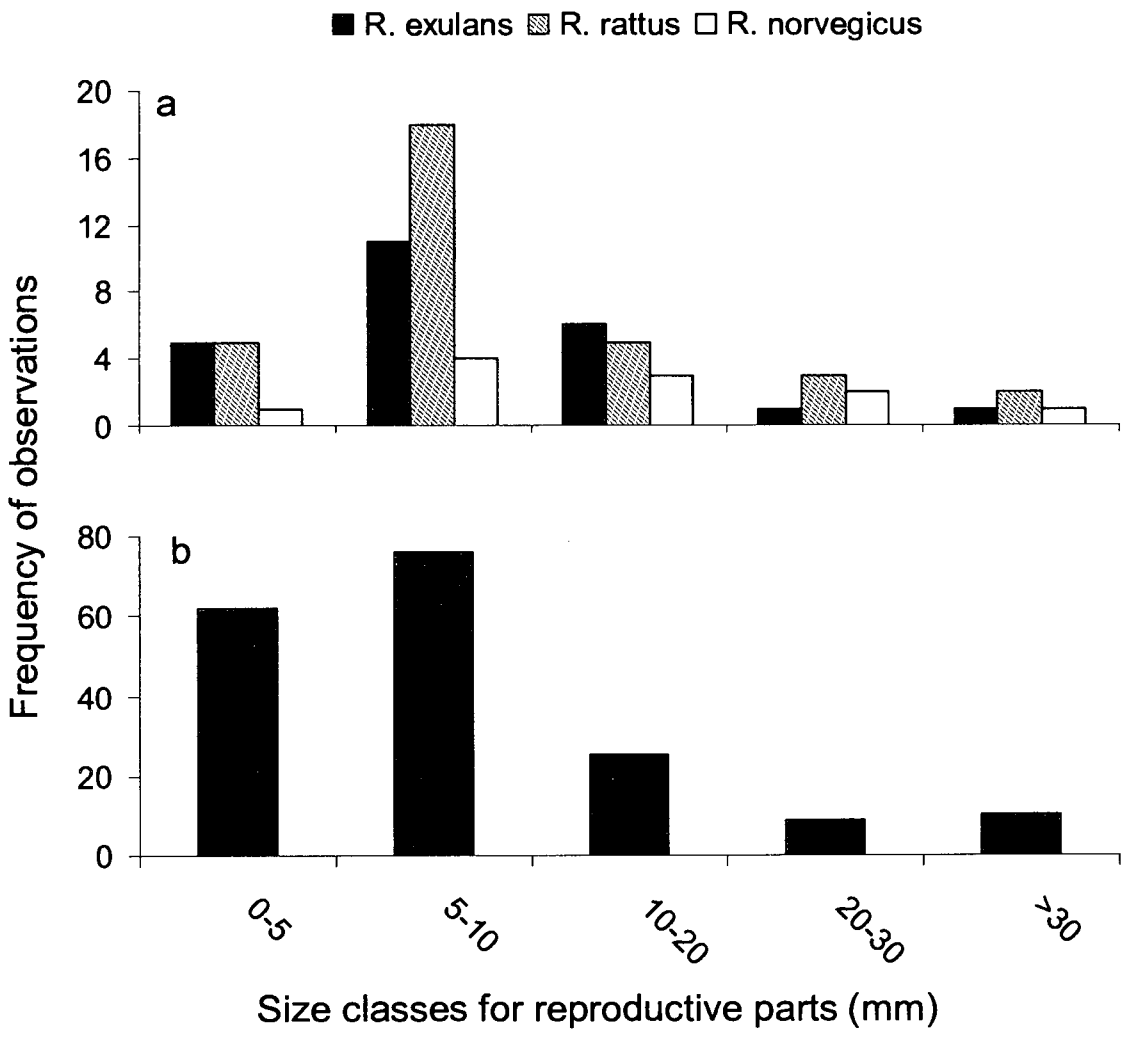
R. exulans
R. rattus
R. norvegicus
a
b
20
16
12
8
4
0
80
60
40
20
0
Frequency of observations
0-5
5-10
10-20
20-30
>30
Size classes for reproductive parts (mm)

Figure 4.2

Appendix 4.1 – List of plant species consumed by the three rat species (*R. exulans, R. rattus, R. norvegicus*) studied including general information about reproductive parts and seeds. Entries in bold indicate consumption of vegetative parts only, not reproductive parts or seeds. '*' indicates flesh of fruit and not seed being consumed. Information about reproductive part and seed size came from the following references: Tutin et al. 2001, Wagner et al. 1990, Webb et al. 1988, Allan 1982, Healy and Edgar 1980, Moore and Edgar 1970, Ohwi 1984, St. John 1960, *http://nzflora.landcareresearch.co.nz/*, *http://plants.usda.gov/* (downloaded September 2008).

Family	Plant species	Rat species	Plant part eaten	Repro. part	Repro. part characteristics
Agavaceae	*Phormium cookianum*	*R. exulans*	flowers, fruit	capsule	dry
Aizoaceae	*Disphyma australe*	*R. exulans*	fruit	capsule	dry
Apocynaceae	*Parsonsia heterophylla*	*R. exulans*	fruit	follicle	fleshy
Aquifoliaceae	*Ilex aquifolium*	*R. exulans*	fruit	fruit	fleshy
Aracaceae	*Rhopalostylis sapida*	*R. exulans*	fruit, rootbases of juveniles	drupe	fleshy
Araliaceae	*Meryta sinclairii*	*R. exulans*	petiole, bark, shoot apex, fruit	drupe	fleshy
Araliaceae	*Pseudopanax arboreus*	*R. exulans*	**bark**	**berry**	**coriaceous**
Araliaceae	*Pseudopanax lessonii*	*R. exulans*	**leaves, petiole, shoot apex**	**berry**	**coriaceous**

Repro. part size	Seed size	Reference	Former name
>100 mm	8-10 mm	Campbell 1978	
1 mm	1 mm	Campbell 1978	
70-150 mm	7-15 mm plus 12-20 mm pappus	Campbell 1978	
6-10 mm	---	Williams et al. 2000	
10 mm	10 mm	Campbell 1978	
10 mm	6-10 mm	Campbell 1978	
---	**3-6 mm**	Campbell 1978	
6-7 mm	**5-7mm**	Campbell 1978	

Arecaceae	*Cocos nucifera*	*R. exulans*	**flower**	**fruit**	**dry**
Aspleniaceae	*Asplenium oblongifolium*	*R. exulans*	**petioles**	**sori**	**dry**
Berberidaceae	*Berberis glaucocarpa*	*R. exulans*	fruit	berry	fleshy
Boraginaceae	*Toumefortia argentea*	*R. exulans*	fruit	globose	dry, corky
Caprifoliaceae	*Leycesteria formosa*	*R. exulans*	fruit	berry	fleshy
Caryophyllaceae	*Silene gallica*	*R. exulans*	fruit	capusle	dry
*Corynocarpaceae	*Corynocarpus laevigatus*	*R. exulans*	flesh of fruit, not seed	drupe	fleshy
Cyperaceae	*Cyperus ustulatus*	*R. exulans*	fruit	nut	dry
Cyperaceae	*Ficinia nodosa*	*R. exulans*	fruit, rootbases	nut	dry
Dryopteridaceae	*Polystichum neozelandicum*	*R. exulans*	**petioles**	**sori**	**dry**
Elaeocarpaceae	*Elaeocarpus dentatus*	*R. exulans*	fruit, bark	drupe	fleshy
Goodeniaceae	*Scaevola sericea*	*R. exulans*	fruit, seed	berry	fleshy
Lauraceae	*Beilschmiedia tarairi*	*R. exulans*	fruit	drupe	fleshy

200-300 mm	**200-300 mm**	Marshall 1955, Fall et al. 1971	
---	---	Campbell 1978	Asplenium lucidum
7-12 mm	---	Williams et al. 2000	
5-8 mm	---	Fall et al. 1971	Messerschmidia argentea
7-10 mm	1-1.5 mm	Williams et al. 2000	
7-10 mm	0.8 mm	Campbell 1978	
20-40 mm	20-40 mm	Campbell et al. 1984	
1.5-2 mm	1.5-2 mm	Campbell 1978	
1 mm	1 mm	Campbell 1978	Scirpus nodosus
---	---	Campbell 1978	Polystichum richardii
18 mm	9-17 mm	Campbell 1978	
5-13 mm	---	Fall et al. 1971, Wirtz 1972	Scaevola taccada
25-35 mm	25-35 mm	Campbell 1978	

Lauraceae	*Beilschmiedia tawa*	*R. exulans*	fruit	drupe	fleshy
Leguminosae	*Sophora tetraptera*	*R. exulans*	**flower**	**pod**	**dry**
Loganiaceae	*Geniostoma rupestre*	*R. exulans*	**bark**	**capsule**	**dry**
Malvaceae	*Hoheira populnea*	*R. exulans*	**bark**	**mericarp and wing**	**dry**
Meliaceae	*Dysoxylum spectabile*	*R. exulans*	fruit	capsule	fleshy
Mimosaceae	*Paraserianthes lophantha*	*R. exulans*	fruit	pod	dry
*Monimiaceae	*Hedycarya arborea*	*R. exulans*	flesh of fruit, not seed	drupe	fleshy
Moraceae	*Streblus banksii*	*R. exulans*	fruit, bark	drupe	fleshy
Myrtaceae	*Metrosideros excelsa*	*R. exulans*	**flowers**	**seed**	**dry wind dispersed**
Nothofagaceae	*Nothofagus solandri var. solandri*	*R. exulans*	fruit	nut	dry
Oleaceae	*Ligustrum sinense*	*R. exulans*	fruit	globose	fleshy

20-30 mm	20-30 mm	Campbell 1978	
up to 200 mm	**6-8 mm**	Campbell 1978	
5-10 mm	**1-1.5 mm**	Campbell 1978	
7-16 mm	4-7 mm	Campbell 1978	
25 mm	10-12 mm	Campbell 1978	
80-150 mm	7 mm	Campbell et al. 1984	Albizia lophanthus
15 mm	9-14 mm	Campbell et al. 1984	
5-6 mm	5-6 mm	Campbell 1978	Paratrophis banksii
3-5 mm	**3-5 mm**	Campbell 1978	
5-7 mm	5-7 mm	Campbell 1978	
4-6 mm	3-4 mm	Williams et al. 2000	

Oleaceae	*Nestegis cunninhamii*	*R. exulans*	fruit	drupe	fleshy
Passifloraceae	*Passiflora tetrandra*	*R. exulans*	fruit	berry and aril	fleshy
Piperaceae	*Macropiper excelsum*	*R. exulans*	fruit, leaf petoiles, twigs	drupe many close set	fleshy
Pittosporaceae	*Pittosporum crassifolium*	*R. exulans*	fruit	subglobose capsule	fleshy
Poaceae	*Anthoxanthum odoratum*	*R. exulans*	fruit	spikelet	dry
Poaceae	*Bromus catharticus*	*R. exulans*	fruit	spikelet	dry
Poaceae	*Dactylis glomerata*	*R. exulans*	fruit	spikelet	dry
Podocarpaceae	*Dacrycarpus dacrydioides (A.Rich) de Laub (1969)*	*R. exulans*	fruit	*nut and* succulent peduncle	fleshy and dry

12-17 mm	10-17 mm	Campbell 1978, Sweetapple and Nugent 2007	
250-300 mm	6-8 mm	Campbell 1978	
2-3 mm drupe closeset	1.5-2.5 mm	Campbell 1978, Williams et al. 2000	
20-30 mm	3-6 mm	Campbell 1978	
7-9.5 mm	---	Campbell 1978	
20-40 mm	11-20 mm	Campbell et al. 1984	Bromus unioloides, B. willdenowii
6-8 mm	4-8 mm	Campbell 1978	
6-11 mm	4-5 mm	Campbell 1978	Podocarpus dacrydioides

Podocarpaceae	*Prumnopitys ferruginea (D.Don) de Laub. (1978)*	*R. exulans*	fruit	fruit	fleshy
Proteaceae	*Knightia excelsum*	*R. exulans*	fruit	seed with wing	dry
Roseaceae	*Cotoneaster glaucophyllus*	*R. exulans*	fruit	fruit	fleshy
*Roseaceae	*Crataegus monogyna*	*R. exulans*	flesh of fruit, not seed	fruit	fleshy
Roseaceae	*Pyracantha angustifolia*	*R. exulans*	fruit	fruit	fleshy
Rubiaceae	*Coprosma grandifolia*	*R. exulans*	fruit, bark	drupe	fleshy
Rubiaceae	*Coprosma macrocarpa*	*R. exulans*	fruit, bark, twigs, seedlings	drupe	fleshy
Rubiaceae	*Coprosma repens*	*R. exulans*	fruit, bark	drupe	fleshy
Rubiaceae	*Coprosma rhamnoides*	*R. exulans*	**bark**	**drupe**	**fleshy**
Rubiaceae	*Guettarda speciosa*	*R. exulans*	fruit	woody	dry
Rubiaceae	*Morinda*	*R. exulans*	fruit	syncarp	fleshy

20 mm	11-17 mm	Campbell 1978	Podocarpus ferrugineus
20-40 mm	8-14 mm	Campbell 1978	
5-9 mm	—	Williams et al. 2000	
7-11 mm	—	Williams et al. 2000	
4-7 mm	—	Williams et al. 2000	
7-9 mm	4-8 mm	Campbell 1978, Williams et al. 2000	Corposma australis
10-25 mm	3-5 mm	Campbell 1978	
10 mm	3-8 mm	Campbell 1978	
3-4 mm	**2-4 mm**	Campbell 1978	
10-40 mm	1-5 mm	Fall et al. 1971, McConkey et al. 2003	
50-100 mm	—	Fall et al.	

	citrifolia				
Sapotaceae	*Pouteria coustata*	*R. exulans*	fruit	berry	fleshy
Scrophulariaceae	*Hebe parviflora*	*R. exulans*	**bark**	**raceme**	**dry**
Smilacaceae	*Ripogonum scandens*	*R. exulans*	fruit, shoot, rootbases of juvelines	globose ovary	fleshy
Solonaceae	*Lycium ferocissimum*	*R. exulans*	fruit	fruit	fleshy
Tiliaceae/ Malvaceae	*Triumfetta procumbens*	*R. exulans*	fruit and seeds	capsule	dry
Verbenaceae	*Vitex lucens*	*R. exulans*	flowers, fruit	drupe	fleshy
Violaceae	*Melicytus ramiflorus*	*R. exulans*	leaf lamina, seedlings, fruit, bark	berry	fleshy
Aizoaceae	*Carpobrotus aff. Acinaciformis*	*R. rattus*	seed	drupe	fleshy
Aizoaceae	*Carpobrotus edulis*	*R. rattus*	seed	fruit	fleshy
Apocynaceae	*Ochrosia nakaiana*	*R. rattus*	fruit	—	—

1971

21-26 mm	21-26 mm	Campbell 1978	Planchonella novo-zelandica
30-50 mm	**<1 mm**	Campbell 1978	
10 mm	—	Campbell 1978	
5-14 mm	—	Campbell et al. 1984	
12 mm	—	Marshall 1955, Fall et al. 1971	
20 mm	8-15 mm	Campbell 1978	
4-5 mm	1.5-2.5 mm	Campbell 1978, Williams et al. 2000	
—	—	Bourgeois et al. 2005	
20-35 mm	—	Bourgeois et al. 2005	
—	—	Abe 2007	

Aracaceae	*Rhopalostylis sapida*	*R. rattus*	fruit, rootbases of juveniles	drupe	fleshy
Araliaceae	*Pseudopanax arboreus*	*R. rattus*	**bark**	**berry**	**coriaceous**
Araliaceae	*Schefflera digitata*	*R. rattus*	**bark**	**fruit**	**fleshy**
Araliaceae	*Stilbocarpa lyallii*	*R. rattus*	**leaves, stems, roots**	**fruit**	**fleshy**
Arecaceae	*Cocos nucifera*	*R. rattus*	fruit	fruit	dry
Asteraceae	*Olearia lyallii*	*R. rattus*	**buds**	**achene**	**dry**
Berberidaceae	*Berberis glaucocarpa*	*R. rattus*	fruit	berry	fleshy
Boraginaceae	*Tournefortia argentea*	*R. rattus*	fruit	mericarp	dry, corky

10 mm	10 mm	Campbell 1978, Campbell et al. 1984
---	**3-6 mm**	Campbell 1978
3-5 mm	**2-3 mm**	Campbell 1978, Sweetapple and Nugent 2007
3-5 mm	**2-3 mm**	Campbell 1978
200-300 mm	200-300 mm	Marshall 1955, Fall et al. 1971
7 mm	**6-8 mm plus 2-3 mm pappus**	Campbell 1978
7-12 mm	---	Williams et al. 2000
5-7 mm	---	Fall et al. 1971

Caprifoliaceae	*Leycesteria formosa*	*R. rattus*	fruit	berry	fleshy
Caprifoliaceae	*Viburnum tinus*	*R. rattus*	fruit	drupe	fleshy
Combretaceae	*Terminalia catappa*	*R. rattus*	fruit	nut	dry
Corynocarpaceae	*Corynocarpus laevigatus*	*R. rattus*	fruit	drupe	fleshy
Elaeocarpaceae	*Aristotelea serrata*	*R. rattus*	fruit	fruit	fleshy
Elaeocarpaceae	*Elaeocarpus dentatus*	*R. rattus*	fruit	drupe	fleshy
Elaeocarpaceae	*Elaeocarpus hookerianus*	*R. rattus*	fruit	drupe	fleshy
Goodeniaceae	*Scaevola sericea*	*R. rattus*	fruit	berry	fleshy
Lauraceae	*Laurus azorica*	*R. rattus*	fruit	berry	fleshy
Lauraceae	*Neolitsea sericea*	*R. rattus*	fruit	berry	fleshy
Lauraceae	*Persea indica*	*R. rattus*	fruit	berry	fleshy
Liliaceae	*Astelia solandri*	*R. rattus*	fruit	globose ovary	fleshy

7-10 mm	1-1.5 mm	Williams et al. 2000	
8 mm	---	Delgado Garcia 2000	
---	---	Abe 2007	
20-40 mm	20-40 mm	Campbell 1978	
4-5 mm	2-3 mm	Sweetapple and Nugent 2007	
18 mm	9-17 mm	Campbell 1978	
8 mm	6-8 mm	Sweetapple and Nugent 2007	
5-13 mm	---	Fall et al. 1971	Scaevola taccada
10-15 mm	---	Delgado Garcia 2000	
12-15 mm	---	Abe 2007	
20 mm	---	Delgado Garcia 2000	
4-5 mm	<2 mm	Campbell 1978	

Liliaceae	*Collospermum hastatum*	*R. rattus*	fruit	mucilaginous aril	fleshy
Liliaceae	*Collospermum microspermum*	*R. rattus*	fruit	fruit	fleshy
*Monimiaceae	*Hedycarya arborea*	*R. rattus*	flesh of fruit, not seed	drupe	fleshy
Myrsinaceae	*Myrsine salicina*	*R. rattus*	seed	fruit	fleshy
Nothofagaceae	*Nothofagus truncata*	*R. rattus*	fruit	nut	dry
Oleaceae	*Ligustrum sinense*	*R. rattus*	fruit	globose	fleshy
Onagraceae	*Fuchsia excorticata*	*R. rattus*	fruit	berry	fleshy
Orchidaceae	*Gastrodia cunninghamii*	*R. rattus*	**rootbase**	**seed or rhizome**	**—**
Palmae	*Livistona boninensis*	*R. rattus*	fruit	—	—
Pandanaceae	*Pandanus boninensis*	*R. rattus*	fruit	—	—

4.5 mm	<1 mm	Campbell 1978
4.5 mm	1 mm	Sweetapple and Nugent 2007
15 mm	9-14 mm	Campbell 1978, Campbell et al. 1984
5-9 mm	5-6 mm	Sweetapple and Nugent 2007
7-9 mm	7-9 mm	Campbell 1978
4-6 mm	3-4 mm	Williams et al. 2000
10 mm	0.7-0.9 mm	Sweetapple and Nugent 2007
---	---	Campbell 1978
---	---	Abe 2007
---	---	Abe 2007

Passiflorace ae	*Passiflora mollisima*	*R. rattus*	fruit	fruit	fleshy
Passiflorace ae	*Passiflora tetrandra*	*R. rattus*	fruit	berry and aril	fleshy
Piperaceae	*Macropiper excelsum*	*R. rattus*	fruit (seeds intact)	drupe	fleshy
Pittosporace ae	*Pittosporum hosmeri*	*R. rattus*	seeds	capsule	fleshy
Poaceae	*Poa litorosa*	*R. rattus*	**leaf bases**	**spikelet**	**dry**
Podocarpace ae	*Dacrycarpus dacrydioides (A.Rich) de Laub (1969)*	*R. rattus*	fruit	nut and succulent peduncle	fleshy and dry
Podocarpace ae	*Dacrydium cupressinum*	*R. rattus*	fruit, seedlings	nut on enlarged peduncle (dry or fleshy)	fleshy and dry
Podocarpace ae	*Podocarpus hallii*	*R. rattus*	fruit	nut on succulent peduncle	fleshy and dry

6-12 mm	4.5-5.5 mm	Williams et al. 2000
250-300 mm	6-8 mm	Campbell 1978
2-3 mm	1.5-2.5 mm	Campbell 1978, Williams et al. 2000
30-80 mm	7-10 mm	Cuddihy and Stone 1990
7-14 mm	---	Campbell 1978
6-11 mm	4-5 mm	Campbell 1978
6-11 mm	3-5 mm	Campbell 1978, Sweetapple and Nugent 2007
10-17 mm	6-7 mm	Campbell 1978

Podocarpaceae	*Prumnopitys ferruginea (D.Don) de Laub. (1978)*	*R. rattus*	fruit	fruit	fleshy
Podocarpaceae	*Prumopitys taxifolia (D.Don) de Laub. (1978)*	*R. rattus*	fruit	drupe	dry
Roseaceae	*Cotoneaster glaucophyllus*	*R. rattus*	fruit	fruit	fleshy
Roseaceae	*Cotoneaster simonsii*	*R. rattus*	fruit	fruit	fleshy
*Roseaceae	*Crataegus monogyna*	*R. rattus*	flesh of fruit, not seed	fruit	fleshy
Roseaceae	*Pyracantha angustifolia*	*R. rattus*	fruit	fruit	fleshy
Roseaceae	*Rubus cissoides*	*R. rattus*	fruit	druplets	fleshy
Rubiaceae	*Coprosma grandifolia*	*R. rattus*	fruit	drupe	fleshy
Rubiaceae	*Coprosma lucida*	*R. rattus*	fruit	drupe	fleshy

20 mm	11-17 mm	Campbell 1978, Sweetapple and Nugent 2007	
5-9 mm	5-9 mm	Campbell 1978	Podocarpus spicatus
5-9 mm	—	Williams et al. 2000	
5-10 mm	—	Williams et al. 2000	
7-11 mm	—	Williams et al. 2000	
4-7 mm	—	Williams et al. 2000	
—	—	Sweetapple and Nugent 2007	
7-9 mm	4-8 mm	Campbell 1978, Williams et al. 2000	
8-12 mm	5-9 mm	Campbell 1978	

Rubiaceae	*Coprosma robusta*	*R. rattus*	fruit	drupe	fleshy
Rubiaceae	*Coprosma tayloriae*	*R. rattus*	fruit	drupe	fleshy
Rubiaceae	*Guettarda speciosa*	*R. rattus*	fruit, stalks and leaves	woody	dry
Rubiaceae	*Morinda citrifolia*	*R. rattus*	fruit	syncarp	fleshy
Smilacaceae	*Ripogonum scandens*	*R. rattus*	fruit	globose ovary	fleshy
Solonaceae	*Solanum aviculare*	*R. rattus*	fruit	berry	fleshy
Tiliaceae	*Triumfetta procumbens*	*R. rattus*	fruit	capsule	dry
Violaceae	*Melicytus ramiflorus*	*R. rattus*	fruit	berry	fleshy
*Winteracea e	*Pseudowinte ra axillaris*	*R. rattus*	flesh of fruit, not seed	fruit	fleshy
Winteraceae	*Pseudowinte ra colorata*	*R. rattus*	fruit	fruit	fleshy

4-9 mm	2-7 mm	Campbell 1978, Williams et al. 2000
—	2.5-5 mm	Sweetapple and Nugent 2007
10-40 mm	1-5 mm	Fall et al. 1971
50-100 mm	—	Fall et al. 1971
10 mm	—	Campbell 1978
15-25 mm	1-2 mm	Campbell 1978, Williams et al. 2000
12 mm	—	Fall et al. 1971
4-5 mm	1.5-2.5 mm	Campbell 1978, Williams et al. 2000
5-6 mm	2-4 mm	Campbell 1978
3-5 mm	2.5-3.5 mm	Sweetapple and Nugent 2007

Aracaceae	*Rhopalostylis sapida*	*R. norvegicus*	fruit	drupe	fleshy
Araliaceae	*Pseudopanax arboreus*	*R. norvegicus*	**bark**	**berry**	**coriaceous**
Araliaceae	*Schefflera digitata*	*R. norvegicus*	**bark**	**fruit**	**fleshy**
Araliaceae	*Stilbocarpa polaris*	*R. norvegicus*	**heart**	**fruit**	**fleshy**
Araucariaceae	*Agathis australis*	*R. norvegicus*	**seedlings**	**cone**	**dry**
Corynocarpaceae	*Corynocarpus laevigatus*	*R. norvegicus*	fruit	drupe	fleshy
Cupressaceae	*Thuja plicata*	*R. norvegicus*	**plant shoots**	**cone**	**dry**
Elaeocarpaceae	*Elaeocarpus dentatus*	*R. norvegicus*	fruit	drupe	fleshy
Ericaceae	*Gaultheria shallon*	*R. norvegicus*	fruit or seed	fruit	fleshy
Ericaceae	*Vaccinium parvifolium*	*R. norvegicus*	fruit or seed, plant shoots	berry	fleshy
Fagaceae	*Quercus serrata*	*R. norvegicus*	seed	nut	dry
Lauraceae	*Beilschmiedia tawa*	*R. norvegicus*	**seedling**	**drupe**	**fleshy**

10 mm	10 mm	Campbell 1978
---	**3-6 mm**	Campbell 1978
3-5 mm	**2-3 mm**	Campbell 1978
4-6 mm	**2-4 mm**	Campbell 1978
50-60 mm	**7-11 mm**	Campbell 1978
20-40 mm	20-40 mm	Campbell 1978
10-15 mm	---	Drever and Harestad 1998
18 mm	9-17 mm	Campbell 1978
6-10 mm		Drever and Harestad 1998
—	—	Drever and Harestad 1998
10-20 mm	10-20 mm	Cheng et al. 2005
20-30 mm	**20-30 mm**	Campbell 1978

Leguminosae	*Robinia pseudoacacia*	*R. norvegicus*	fruit	pod	dry
Leguminosae	*Trifolium repens*	*R. norvegicus*	**leaves**	**glabrous pod**	**dry**
Monimiaceae	*Hedycarya arborea*	*R. norvegicus*	flesh of fruit	drupe	fleshy
Passifloraceae	*Passiflora tetrandra*	*R. norvegicus*	fruit	berry and aril	fleshy
Phyllocaldaceae	*Phyllocladus trichomanoides*	*R. norvegicus*	**bark**	**nut**	**dry**
Pinaceae	*Picea sitchensis*	*R. norvegicus*	fruit or seed, plant shoots	cone	dry
Pinaceae	*Pinus radiata*	*R. norvegicus*	fruit	winged nut	dry
Pinaceae	*Tsuga heterophylla*	*R. norvegicus*	fruit or seed, plant shoots	cone	dry
Piperaceae	*Macropiper excelsum*	*R. norvegicus*	fruit	drupe many close set	fleshy
Pittosporaceae	*Pittosporum crassifolium*	*R. norvegicus*	fruit	subglobose capsule	fleshy
Poaceae	*Calamagrostis nutkaensis*	*R. norvegicus*	fruit or seed	spike	dry

35-80 mm	—	Campbell 1978
4-5 mm	**1 mm**	Campbell 1978
15 mm	9-14 mm	Grant-Hoffman 2009b
250-300 mm	6-8 mm	Campbell 1978
3 mm	**3 mm**	Campbell 1978
5-10 mm	—	Drever and Harestad 1998
15-20 mm	60-130 mm	Campbell 1978
—	—	Drever and Harestad 1998
2-3 mm drupe closeset	1.5-2.5 mm	Campbell 1978
20-30 mm	3-6 mm	Grant-Hoffman 2009b
—	—	Drever and Harestad 1998

Podocarpaceae	*Dacrycarpus dacrydioides (A.Rich) de Laub (1969)*	*R. norvegicus*	**seedlings**	**nut and succulent peduncle**	**fleshy and dry**
Podocarpaceae	*Dacrydium cupressinum*	*R. norvegicus*	fruit	nut and enlarged peduncle	fleshy and dry
Podocarpaceae	*Podocarpus totara*	*R. norvegicus*	**seedlings**	**nut and enlarged peduncle**	**fleshy**
Podocarpaceae	*Prumnopitys ferruginea (D.Don) de Laub. (1978)*	*R. norvegicus*	fruit, seedlings, bark	fruit	fleshy
Podocarpaceae	*Prumopitys taxifolia (D.Don) de Laub. (1978)*	*R. norvegicus*	fruit	drupe	dry
Rubiaceae	*Coprosma grandifolia*	*R. norvegicus*	fruit	drupe	fleshy
Rubiaceae	*Coprosma macrocarpa*	*R. norvegicus*	fruit	drupe	fleshy
Taxaceae	*Taxus brevifolia*	*R. norvegicus*	**plant shoots**	**seeds plus aril**	**fleshy**
Violaceae	*Melicytus ramiflorus*	*R. norvegicus*	**bark, leaf**	**berry**	**fleshy**

6-11 mm	**4-5 mm**	Campbell 1978
6-11 mm	3-5 mm	Campbell 1978
7-12 mm	**4-5 mm**	Campbell 1978
20 mm	11-17 mm	Campbell 1978
5-9 mm	5-9 mm	Campbell 1978
7-9 mm	4-8 mm	Campbell 1978
10-25 mm	3-5 mm	Grant-Hoffman 2009b
—	**5-6 mm**	Drever and Harestad 1998
4-5 mm	**1.5-2.5 mm**	Campbell 1978

CHAPTER 5: GENERAL DISCUSSION

In Chapters 2 and 3 I found that invasive rats (*Rattus rattus, Rattus norvegicus*) are affecting island vegetation directly through herbivory and indirectly through the reduction and sometimes extirpation of burrowing seabirds (Procellariiformes: petrels, prions, and shearwaters). In Chapter 4 I found that invasive rats may consume more seeds and fruits than vegetative plant parts. The consumption of seeds may be particularly devastating to plant populations as over time reproduction of certain plant species may be hindered, translating into population differences in plants after rat invasion. Indeed, in Chapter 3 I found that on islands where rats (*Rattus rattus, Rattus norvegicus*) have invaded, density and species richness of seeds in litter is lower than on islands with no history of rats. While I found in Chapter 4 that large fruits or seeds with hard seed coats may be less attractive to rats as a food source, these characteristics are deterrents only and may be overcome if the reward is large or other food sources are limited or less attractive. Chemical defenses may be more successful in deterring rat consumption. In addition to consuming seeds I found in Chapter 3 that invasive rats are consuming seedlings, which further contributes to changes in seedling communities.

Rats also consume burrowing seabirds often extirpating entire colonies (see review Jones et al. 2008). I found in Chapter 3 that species richness of germinating seedlings is higher in soils where there is no history of rats and thus higher populations of seabirds. However, observed species richness and seedling density at very high seabird densities is low, due to the physical disturbance of seabirds during burrow formation. The burrowing activity of seabirds does seem to bury seeds and may increase the number of

seeds incorporated into the soil and thus germination rates. While it has been shown in several studies that seabirds affect vegetation through nutrient inputs (see review Ellis 2005), I have found that the physical disturbance of burrowing seabirds is also an important influence on island vegetation.

While not a clear result, Chapter 3 suggests that seabird colonies may provide access points for non-native species. Species that are quick growing and reproduce early may have an advantage over slower growing plants. In the presence of seabirds, on an active colony, adult plants of these species may be scarce, due to intolerance of the extreme physical disturbance associated with seabird burrowing. However, these types of plants may be able to maintain a presence in the seedbank.

When rats are removed and seabird populations are low or absent, we find that islands do not revert to pre-invasion states. Instead I found in Chapter 2 that these islands exhibit low species richness, with communities often dominated by a few quick growing species. Species that recover well may not be consumed by rats, or consumed as seedlings or at later stages and thus able to maintain a presence in the seedbank. They may also benefit from reductions in seabird populations.

RESPONSES OF PLANT SPECIES: A SYNTHESIS

In addition to affecting seedling communities, invasive rats and burrowing seabirds can have dramatic and surprising effects on certain plant species. We found five woody species (*Coprosma macrocarpa, Dysoxylum spectabile, Melicytus novae-zelandiae, Pittosporum crassifolium, Streblus banksii*) for which seedling densities were

low on rat-invaded islands, and three species (*Coprosma macrocarpa, Pittosporum crassifolium, Pseudopanax lessonii*) with high seedling densities after rat eradications or eradication attempts. We more closely examined the responses of these species to all of the experiments performed and observations made to try to determine at what life stage they are affected by either invasive rats or burrowing seabirds. We considered the number of seeds found in the litter and seed traps, and the number of seedlings found in observational counts, germination trials, and exclosure experiments. For species that were available we also considered results from feeding trials with Norway rats. We looked for patterns that indicated a dramatic change from one life history step to the next. We considered responses from three islands, Middle, Motueka, and Whenuakura. These three islands were chosen because they had the most complete data sets and the best-known rat history.

Although we considered seven plant species, numbers of seeds and seedlings were often low, and we found substantial changes between life history stages for only two species: *Pseudopanax lessonii* and *Streblus banksii*. We did not find seeds or seedlings of *Pseudopanax lessonii* on the uninvaded island. In addition, seeds in seed traps and seeds in the litter were at least twice as abundant at lower burrow densities (> 0.09 burrows m^{-1}) than higher burrow densities (>0.19 burrows m^{-1}) on the rat eradicated island. Thus, very high burrow densities appear to be associated with decreases in seed abundance of this species. In addition, on the rat invaded island in the two plots where we found *Pseudopanax lessonii* seedlings we found 35 seedlings of this species inside exclosures versus one seedling outside of exclosures. However, seeds from this species were not

consumed by rats in the feeding trials. Thus, rat consumption appears to impact this species at the seedling and not the seed stage. In contrast, *Streblus banksii* seeds and seedlings were found only on islands with no history of rats. Rat feeding trials with seeds of this species were inconclusive due to removal by an unidentified invertebrate. However, this species appears to produce copious seeds in the presence of burrowing seabirds. On the uninvaded island we found high numbers of seeds in seed traps (mean=333, range 87 to 849 seeds per plot) and in the litter (mean=168, range 68-403). In addition, there were almost 100 times more seedlings of this species inside of exclosures than in control areas on this island (inside=452, outside=5). The species that showed the next most pronounced difference of this type was also found on this island (*Coprosma macrocarpa* with 128 seedlings inside of exclosures versus 7 outside of exclosures).

Since seeds of *Pseudopanax lesonii* are not preferred by rats (low consumption in feeding trials) this species may be able to maintain a presence in the seed bank, especially while adult plants are still present. In addition, this species had lower seeds in seed traps and in the litter at higher burrow densities, and may benefit from lowered numbers of seabirds or complete extirpation of seabirds with rat invasion. *Streblus banksii* may be vulnerable to rats at the seed or seedling stage (Campbell and Atkinson 2002) and potential for recovery after rat eradication was not assessed due to absence of adult plants on invaded islands. While seedlings of this species were reduced in plots with high burrow densities, we found high numbers of seeds in seed traps and litter samples and seed production of this species may be high, compared to other species, at high burrow

densities. The loss of active seabird colonies likely contributes to the inability of *Streblus banksii* to recover after rat eradications.

By examining the responses of these two plant species, I have shown that individual plant species can react very differently to invasive rats and burrowing seabirds. The outcome of the population of a certain plant species depends not only on its general vulnerability to these two driving factors, but also to the life stage at which it is vulnerable. In order to restore a specific plant species after rat eradication or to protect a plant species of concern in the presence of rats, information on what life stage a plant species is vulnerable to which factor, invasive rats or burrowing seabirds, is necessary.

MANAGEMENT IMPLICATIONS

With new rat invasions, invasive plant species should be closely monitored. With the extirpation of seabirds a flush of non-native species may occur if these species are present in the seedbank. Once rats are removed, seabird colonies may need to be restored to maintain certain vegetation types. However, establishment of pre-invasion communities may be hindered by absences from the seedbank or low germination of seedlings. Thus, some plant species may need to be reintroduced. If seabird colonies are present the physical disturbance of these birds may inhibit establishment of new plant species, especially if seed and seedling populations are already low due to legacy effects of rats. Once seedlings reach approximately 75 cm in height, they are less vulnerable to the physical disturbance of seabirds, and protection of seedlings up to this point may greatly increase the rate of recovery of target plant species. Plant secondary metabolites

may deter rat feeding and may be useful in protecting vulnerable seedlings. In addition, if rats cannot be permanently removed from an area, target plant species may be protected by providing more attractive food sources or by protecting seeds and fruits of these species.

FUTURE RESEARCH DIRECTIONS

While I have found that rats are directly affecting vegetation, independently of burrowing seabird effects, more research in this area is warranted. While I have identified some characteristics that may make vegetation more or less attractive to invasive rats, there is still much to be learned about how rats are making consumptive choices.

In addition, separating the effects of invasive rats and burrowing seabirds is necessary to understand how vegetation communities are affected by these two influential factors. Scientists and managers need to understand what processes are influencing specific aspects of the vegetative community. For example, seedling density appears to be driven mostly by the physical disturbance of seabirds. By linking aspects of the vegetative community to specific effects of invasive rats and burrowing seabirds, restoration efforts can be tailored to better address specific concerns or goals. Similarly, a better understanding of how invasive rats and burrowing seabirds affect specific plant species will help in their restoration. For example, increases in seedling recruitment of plant species after rat eradication has often been attributed to a cessation of rat consumption of these species (e.g., Campbell and Atkinson 1999, Campbell 2002).

However, some of these species may be reacting to a lack of seabirds, and rat removal may not cause their recovery without seabird restoration.

This thesis adds to current knowledge of the effects of invasive rats and burrowing seabirds on island vegetation by first confirming that invasive rats and burrowing seabirds are driving island woody vegetation communities. Secondly, while it has been shown that burrowing seabirds can affect vegetation through allochthonous inputs, we have also shown that the physical disturbance of burrowing is an important driver of woody vegetation on islands. We have found that rat consumption of seeds and seedlings is effecting vegetation and have begun to determine what factors are driving rat consumptive choices. By considering specific effects of invasive rats and burrowing seabirds on island vegetation, restoration of vegetative communities on islands can begin to reach success rates of eradication programs.

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